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Harry Soane, 1888.

ELEMENTS OF PHYSIOLOGY.

LONDON:
PRINTED BY SAMUEL BENTLEY,
Dorset-Street, Fleet-Street.

ELEMENTS OF PHYSIOLOGY.

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TRANSLATED FROM THE GERMAN,

WITH NOTES.

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ILLUSTRATED WITH STEEL PLATES, AND NUMEROUS WOOD ENGRAVINGS.

VOL. I.

CONTAINING GENERAL PHYSIOLOGY, THE BLOOD AND CIRCULATING SYSTEM, THE LYMPH AND LYMPHATIC SYSTEM, RESPIRATION, NUTRITION, GROWTH AND REPRODUCTION, SECRETION, DIGESTION, FUNCTIONS OF THE GLANDS WITHOUT EFFERENT DUCTS, EXCRETION, AND THE NERVOUS SYSTEM.

LONDON:

PRINTED FOR TAYLOR AND WALTON,

BOOKSELLERS AND PUBLISHERS TO UNIVERSITY COLLEGE,

28, UPPER GOWER STREET.

1838.

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PRINTED BY SAMUEL BENTLEY,
Dorset Street, Fleet Street.

TRANSLATOR'S PREFACE.

The Translator feels that no other apology is necessary for introducing the present work to the British student of medicine than is afforded by the reputation of its Author as a physiologist, and the high character which the work has acquired, not only in Germany, but throughout Europe. Its translation was suggested to him by Dr. George Burrows, to whom he has on several occasions been indebted for advice always given with the greatest readiness.

To render a faithful version of the original has been the Translator's chief care; but at the same time he has found, that, to make it fitted to the wants of the student, something more was required. In some instances the order in which the facts, and inductions from them, are stated, has been altered, that their connection might be easier of comprehension. In other cases it has been deemed advisable to omit from the text, and to place in the form of notes, discussions on subjects which, though interesting in themselves, did not appear to come within the limits of what is necessary or desirable in a text-book on Human physiology, particularly when they formed a digression which tended to interfere with the course of the student's reading; some few paragraphs have been entirely omitted, chiefly with the view of avoiding unnecessary repetition. To facilitate the labours of the student, likewise, the paragraph where a new topic commences has been headed with a short statement of this in italics. Steel plates and woodcuts, which, the Translator hopes, will be found useful, have also been added.*

The additions made by the Translator consist almost entirely of newly-discovered facts, and are consequently, on account of the

* The subjects for the woodcuts were drawn on the wood by Mr. W. Bagg, and engraved under his direction.

completeness of the original work at the time of its publication in 1835, few in number; they are distinguished by being included in brackets.

In reducing the numbers from the French to the English standard of measurement, an English inch has been regarded as $\frac{12}{13}$ of a French inch; an English cubic inch as $\frac{100}{121}$ of a French cubic inch.

The Translator cannot too strongly express his grateful acknowledgements for the very kind and valuable assistance that he has received from Dr. Sharpey, Dr. R. Willis, and Mr. Quain: their advice has mainly guided him in the execution of his task, and he has derived confidence from the consciousness of having such friends willing to aid him.

He avails himself, also, with much pleasure, of this opportunity of acknowledging the many marks of kindness and friendship which he has experienced at the hands of Dr. P. M. Latham, and for which he must always retain a sense of gratitude.

56, *Devonshire Street.*

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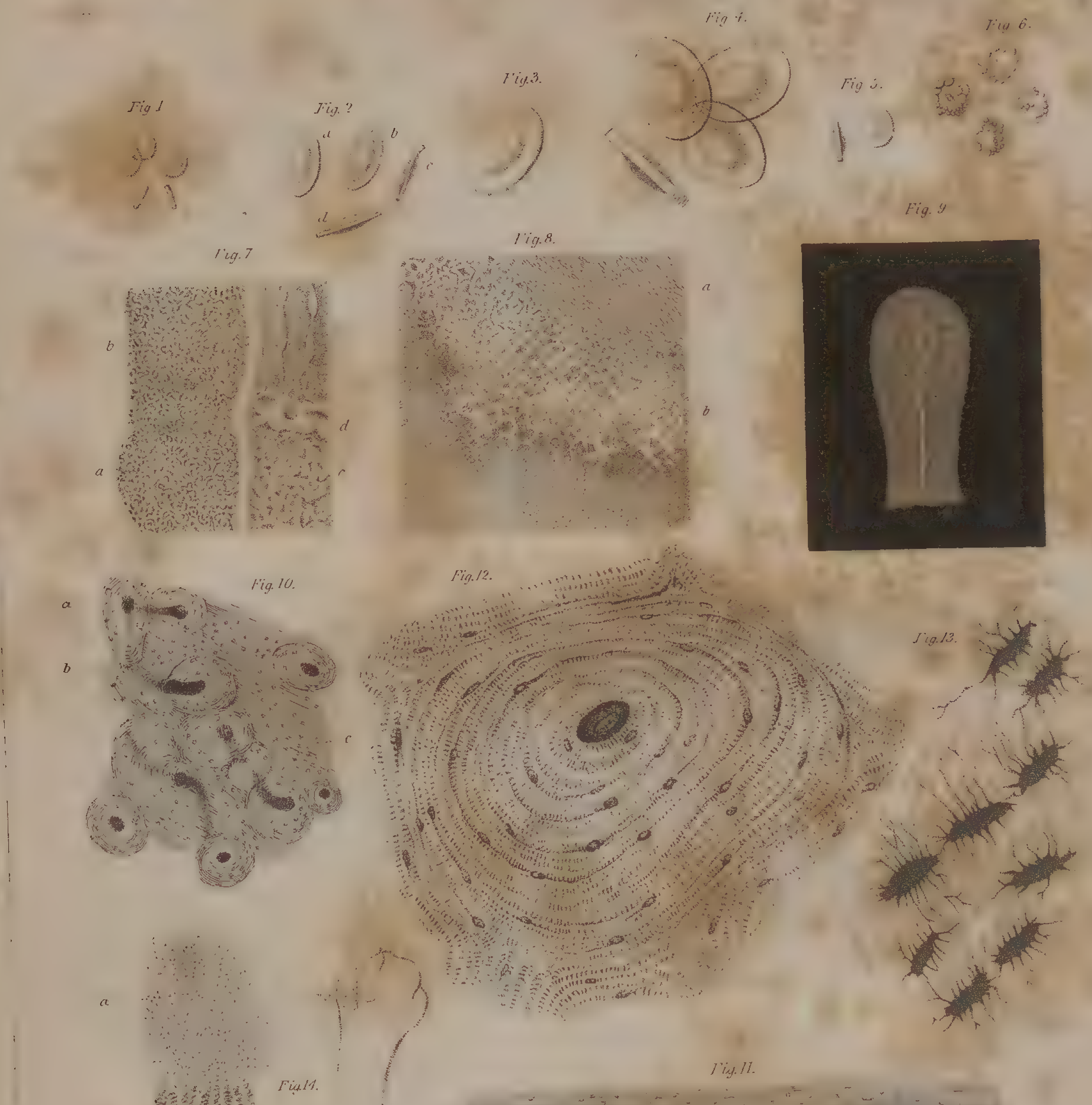

London: Taylor & Walton, Upper Gower Street, 1837

EXPLANATION OF THE PLATE.

[Fig. 1 to 6 represent the particles from the blood of different animals, all magnified about four hundred diameters.

Fig. 1; see page 99 to 109. Red particles of human blood, after Wagner.

Fig. 2. Red particles of the blood of the common fowl. *a*, Ordinary appearance when the flat surface is turned towards the eye; *b*, appearance which is sometimes presented by the particle when in the same position, and which suggests the idea of a furrow surrounding the central nucleus; *c*, *d*, different appearances of the particles when seen edgeways.

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Fig. 5. ———— of the lophius piscatorius, after Wagner.

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Fig. 7. Lymphatics of the glans penis and prepuce, after Breschet. *a*, Superficial layer of lymphatics on the glans; *b*, the same on the prepuce; *c*, deep layer on the glans; *d*, large lymphatics surrounding the base of the glans. (See page 264.)

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Fig. 13. Osseous corpuscules, very much magnified, with the ramifying lines that issue from them, after Müller, in a paper appended to Miescher's dissertation, De inflam. oss. eorumque anat. (See page 379.)

Fig. 14. Thin lamina from the ossifying epiphysis of the humerus of a fœtal calf, taken from a section made perpendicularly to the ossifying surface, as shown in the outline sketch of the bone, and highly magnified. *a*, Uniform granular cartilage; *b*, cartilage nearer to the ossifying surface, the corpuscules aggregated into cells or columns; *c*, bone shooting into the cartilage.

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Fig. 16 represents the appearance in thin laminæ of the cartilage of the epiphysis taken from near the ossifying surface, and magnified, but less highly than the two preceding figures. *a*, *a*, Sections of the canals in which blood-vessels run; *b*, communication between two of these canals; the corpuscules are seen to be collected into groups which are arranged in a radiated manner around the canals. (See page 383.)]

CORRIGENDA ET ADDENDA.

Page 110, in the note, *for* "Dr. Gordon, also, in his Syllabus of Lectures on Anatomy," *read*, "Dr. Gordon, also, in his Outlines of Lectures on Human Physiology, published in 1817, page 60." (The paragraph in Dr. Gordon's Outlines referred to in the note is the following: Venous blood "is discovered by the microscope to consist of two parts; a transparent fluid, and red particles. A, The transparent fluid begins to suffer a species of decomposition called coagulation the moment it escapes from the veins of the living body, and therefore cannot be examined in its natural state. Its properties judged of by an examination of the products of this decomposition. These products are serum and fibrin.")

Page 160. Fig. 5. The vessels distinguished by the cypher 8 are veins which return the blood from the muscles of the back, and pour it into the afferent renal vein (9).

Page 252. Heading of page; *for* "Absorption of the skin," *read* "Absorption by the skin."

CORRIGENDA.

Page 87, line 4, *for* " Dr. Marshall Hall," *read* " Dr. E. Hale."

Page 212, the paragraph at line 28, " This can be seen distinctly in the water salamander." to precede, instead of following, the paragraph, " At the extremity of each of the villi," &c. at line 26.

Page 477, lines 14 and 16, *for* " Nova Scotia," *read* " New Caledonia."

Page 486, line 27, *for* " animals are best able," *read* " animals are least able."

Page 526, line 3, *for* " goat," *read* " horse."

PROLEGOMENA

ON GENERAL PHYSIOLOGY.

Physiology is the science which treats of the properties of organic bodies, animal and vegetable, of the phenomena they present, and of the laws which govern their actions. Inorganic substances are the objects of other sciences, — physics and chemistry.

In entering upon the study of physiology, the first point to be ascertained regards the distinctions between these two great classes of bodies—the organic and the inorganic,—and the following questions suggest themselves for discussion. Do organic and inorganic substances differ in their material composition? and since the phenomena presented by these two classes are obviously so different, are the forces or principles on which they depend, also different; or are the forces which give rise to the phenomena of the organic kingdom merely modifications of those which produce physical and chemical actions?

1. *Of Organic Matter.*

Nothing analogous to sensation, nutrition, or generation, is presented by inorganic bodies, and nevertheless the matter which composes organic bodies consists of precisely the same elements as inorganic matter. In examining the composition of organised bodies, it is true, we meet with substances—the proximate principles, or *principes immediats*—which are peculiar to organic bodies, and cannot be produced artificially by any chemical process; such are fibrin, albumen, gelatin, &c. But all these substances may be reduced by chemical analysis to the same simple elements which constitute minerals. Of these simple substances, all entering into the composition of inorganic bodies, there are fifty-two. In organic bodies there have been discovered but eighteen.

The elementary substances which are met with in plants are:

1. Carbon, 2. Oxygen, 3. Hydrogen,	their most essential components.
4. Nitrogen,	found less frequently.
5. Phosphorus, 6. Sulphur,	. . principally in vegetable albumen and gums, especially in the tetradynamia, combined with nitrogen.
7. Potassium,	. . almost universally.
8. Sodium,	. . principally in marine plants.

9. Calcium, found almost universally.
10. Aluminium, . . rarely.
11. Silicium.
12. Magnesium, occurring rarely.
13. Iron, }
14. Manganese, } . . frequently.
15. Chlorine.
16. Iodine, }
17. Bromine, } . . in marine plants.

The same substances, with the exception of aluminium, are met with likewise in the animal kingdom. Here sodium is more frequent, the potassium less frequent than in plants; iodine and bromine occur in some marine animals.

In man and the higher animals the components are:

1. Oxygen.
2. Hydrogen.
3. Carbon.
4. Nitrogen.
5. Sulphur, met with principally in the hair, albumen, and brain.
6. Phosphorus, ... in the bones, teeth, and brain.
7. Chlorine, }
8. Fluor, }
9. Potassium, }
10. Sodium, } . . . . in the teeth and bones.
11. Calcium, }
12. Magnesium, }
13. Manganese, }
14. Silicium, } found in the hair.
15. Iron, . . in the blood, pigmentum nigrum, and crystalline lens.

[Copper is also numbered among the substances which sometimes enter into the composition of organic bodies. Beecher asserts that he has found gold also in the ashes of tamarinds.*]

The number of the elements which enter into their composition, constitutes, then, the first difference between organic and inorganic bodies. All the elementary substances found in the inorganic kingdom do not enter into the composition of organic bodies; some are even inimical to their life.

The mode in which the elements are combined forms a second distinguishing character; and the peculiarity of organic matter depends probably on the following circumstances, first pointed out by Berzelius and Fourcroy.

1. In mineral substances the elements are always combined in a binary manner; thus, two elementary substances unite together, and this binary compound unites again with another simple substance, or with another binary compound. For example, carbonate of ammonia is

* Tiedemann's Physiology, translated, with notes, by Drs. James Manby Gulley, and J. Hunter Lane, p. 6.

constituted of carbon, oxygen, hydrogen, and nitrogen, combined as follows:

Carbon, Oxygen,	unite to form carbonic acid,	which again unite to form carbonate of ammonia.
Hydrogen, Nitrogen,	.. .. ammonia,	

In minerals the elementary substances are never observed to combine three or four together, so as to form a compound in which each element is equally united with all the others. This, however, is universally the case in organic bodies. Oxygen, hydrogen, carbon, and nitrogen, the same elements which by binary combination formed inorganic substances, unite together, each with all the others, and form the peculiar proximate principles of organic beings. These compounds are termed ternary, or quaternary, according to the number of elements composing them. Vegetable mucus, starch, and adipose matter are ternary compounds of oxygen, carbon, and hydrogen: gum, albumen, fibrin, animal mucus, and resin are quaternary compounds, their fourth ingredient being nitrogen.

A doubt has recently been thrown upon this theory of the composition of organic substances, especially with respect to some particular products, such as alcohol; but there is still great probability in its favour, and more particularly in reference to the higher organic compounds, such as albumen, fibrin, &c.*

It must at any rate be admitted, that the mode in which the ultimate elements are combined in organic bodies, as well as the energies by which the combination is effected, are very peculiar; for, although they may be by analysis reduced to their ultimate elements, they cannot be regenerated by any chemical process.

* Berard, Proust, Dobereiner, and Hatchett believe that they have succeeded in producing organic compounds by artificial processes; but their results have not been sufficiently confirmed. Woehler's experiments afford the only trustworthy instances of the artificial formation of these substances. Woehler discovered that a watery solution of ammonia, after being saturated with cyanogen, contained a considerable quantity of oxalic acid. Again, in the preparation of potassium from charcoal and carbonate of potash, a black mass passes over with the metal, which, when treated with water, yields a large proportion of oxalic acid. Oxalic acid, however, is now regarded as a binary compound of carbon and oxygen; the fact that it undergoes decomposition when its water of crystallization is extracted, is no proof to the contrary, for nitric acid also is decomposed by the extraction of the last portion of its water. See Mitscherlich's Chemie, p. 416. Woehler also finds, that urea is obtained in place of cyanite of ammonia, when a solution of chloride of ammonia is poured over freshly precipitated cyanite of silver, chloride of silver being formed at the same time. Urea is also formed in the decomposition of cyanite of lead by solution of ammonia. The solution at first contains cyanite of ammonia; but, by evaporation of the fluid, this salt is converted into urea. In the same way, also, when cyanous acid is mixed with water or liquid ammonia, cyanite of ammonia is first formed, and thence urea. — Gmelin's Chemie, vol. iii. p. 6; Berzelius, Thierchemie, p. 356. Urea, however, can be scarcely considered as organic matter, being rather an excretion than a component of the animal body. It has not perhaps the characteristic properties of organic products.

2. Another essential distinction pointed out by Berzelius is, that in organic products the combining proportions of their elements do not observe a simple arithmetical ratio. Thus, for example, there is a large number of different kinds of fatty matters which Chevreul has examined, and many of which, according to his experiments, differ only by fractional parts in the numerical proportions of their atoms.

3. Organic bodies consist chiefly of combustible matter, which, both in animals and vegetables, is constituted (the acids excepted) of carbon and hydrogen, combined with oxygen in quantity not sufficient to saturate the other elements.*

Tendency to decomposition.—The matter forming organic bodies has a constant tendency to undergo decomposition; it is only the continuance of life which preserves it. But even during life the balance, which maintains its elements in their peculiar combination, may be destroyed by the agency of certain simple inorganic bodies, or binary compounds of these, as we witness in the burning of parts of the living body. At some period or other this change necessarily ensues spontaneously in every living being; the state or influence which maintains the elements in their peculiar combinations becomes more and more feeble, and is, at length, no longer able to counteract the tendency of these elements to form binary compounds among themselves, and with other simple substances in the atmosphere around them. Organic matter is thus annihilated, and with it the organised being of which it formed part. And in ceasing to present the phenomena of life, it falls under the influence of the laws which govern the formation of chemical compounds, presenting the phenomena of fermentation and putrefaction, a foul smell being produced when the substance contained much nitrogen. Chemical compounds, we know, are regulated by the intrinsic properties and the elective affinity of the substances uniting to form them; in organic bodies, on the contrary, the power which induces and maintains the combination of their elements does not consist in the intrinsic properties of these elements, but is something else, which not only counteracts these affinities, but effects combinations in direct opposition to them, and conformably to the laws of its own operation. Light, heat, and electricity, it is true, influence the compositions and decompositions going on in organic bodies, as they do those in inorganic bodies; but nothing justifies us in regarding without further inquiry any one of the imponderables,—namely, heat, light, and electricity,—as the final cause of vital actions.

After the cessation of life, organic substances always undergo decomposition, if the conditions necessary for the exertion of chemical affinity

* These distinctive characters of organic matter will be found more fully detailed in the classical text-books, of chemistry by Berzelius and Gmelin, and of anatomy by Weber in his fourth edition of Hildebrandt's Anatomie des Menschen, vol. i.

are present. The products of this decomposition are nitrogen and hydrogen, (which partly escape in a free state,) water, carbonic acid, carburetted hydrogen, olefiant gas, ammonia, cyanogen, prussic acid, phosphuretted hydrogen, and hydrosulphuric acid; while in some cases the elements reunite in different proportions so as to form a new organic compound, as in the production of sugar from starch in the saccharine fermentation. Sometimes from one organic substance two new compounds are generated,—one organic, the other inorganic,—as in vinous fermentation, during which carbonic acid and alcohol are formed from sugar. Decomposition does not commence in the bodies of animals and plants immediately after their death. This Gmelin explains by supposing that the conditions necessary for the exertion of elective affinity are not then present, just as several inorganic substances require a certain temperature for their decomposition.*

The conditions more or less necessary for the spontaneous decomposition of organic matter, are moisture, the access of atmospheric air, and a certain temperature. The first is absolutely necessary; organic substances when perfectly dry do not undergo decomposition at the ordinary temperature of the atmosphere. Air is also often necessary, but not always; moist animal tissues suffer decomposition even when atmospheric air is excluded, although the presence of air facilitates putrefaction in the highest degree, even more than oxygen. A certain temperature is always necessary.

The gaseous products of the decomposition of animal matter, and of the human body in particular, are carbonic acid, sometimes nitrogen, hydrogen, sulphuretted hydrogen, phosphuretted hydrogen, and ammonia. Acetic acid is also formed, and sometimes nitric acid. The solid matter that remains, consists of the carbonaceous matters, which decompose more slowly, and the fixed mineral ingredients, earths, oxides, and salts, which with the carbonaceous matters form the soil (humus).† Several parts of the bodies of man and animals immersed in water, or buried in certain situations, even without the access of water, undergo a peculiar change, being converted into a substance, named adipocire. Berzelius is of opinion, that the fibrin, albumen, and colouring matter of the blood, as well as the adipose matter, may be converted into this substance; while Gay Lussac and Chevreul state that the fat, which can be extracted from fresh animal textures by chemical processes, equals in quantity the adipocire generated by putrefaction in water, and infer, therefore, that the fat merely is converted into adipocire, while the other tissues are destroyed.

State in which mineral components exist in organic bodies.—The proportions in which the oxygen, hydrogen, carbon, and nitrogen are combined, seem to constitute the chief differences in the composition of

* Gmelin's Chemie, vol. iii. p. 9.

† See Weber loc. cit. vol. i. p. 70.

organic substances. The organic compounds of these elements especially, are ternary and quaternary, not binary. In what state the less abundant mineral ingredients exist in organic bodies,—whether they likewise enter into the formation of ternary or quaternary compounds, or are merely mingled with them in the binary form,—is an important question which cannot at present be determined. Engelhardt has ascertained that the mineral ingredients can be separated from a watery solution of the colouring matter of the blood, and other animal matters, by means of chlorine. From this fact, and from the iron not being extracted by acids, Berzelius infers it to be probable that the iron in the blood is in the metallic state, not in that of oxide; for chlorine has a very strong affinity for metals, and not for oxides, for which acids on the other hand have a great affinity. Professor Henry Rose adduced some experiments which seemed to show that the iron was combined as an oxide with the animal matter, thus as an albuminate of the oxide; but Berzelius again rejects this idea, for in that case the oxide ought to be extracted by acids from the blood as it is from artificially formed albuminate of iron.*

Berzelius cannot decide in what form sulphur and phosphorus exist in animals; whether united with other simple substances to multiple organic compounds, or combined with the ternary compounds of other simple substances so as to form secondary binary compounds, or whether each of these substances, already in a binary form, is again combined with other substances. Vauquelin, by burning the fatty matter of the brain, obtained a cindery mass, which contained so much phosphoric acid, that this latter substance by preventing the access of air arrested the combustion; on removing the phosphoric acid by means of water, the mass again burned for a time, until more acid was formed upon the surface. From this circumstance we see, says Berzelius,† that this cinder contains phosphorus in a fixed, not volatile state,—in a state hitherto unknown in inorganic nature.

Many circumstances, however, render it probable that several mineral substances in the binary form, as salts or oxides, exist in the animal body, either mixed or chemically combined with the animal matter. These circumstances are: 1. the appearance of minute microscopic crystals in the animal fluids simply evaporated; 2. the facility with which the mineral substances contained in plants vary with their situation, which could not be the case if the mineral elements existed in them merely as elements of the organic compounds; 3. the facility with which salts, which enter the blood accidentally, are separated from

* [The arguments of Rose, Engelhardt, and Berzelius, on this point, are stated fully in the section on the Chemical analysis of the blood; the translator, therefore, considered it unnecessary to give them here at length.]

† Thierchemie, p. 16.

it in the urine; 4. that chloride of sodium can, as Autenrieth remarks, be separated from solid animal matter by mere washing; 5. the state of the phosphate of lime in the bones. Professor E. H. Weber shows clearly, that the phosphate of lime of the bones does not exist in them as phosphorus, oxygen, and calcium; but that it is in the state of a salt combined—perhaps only mechanically mixed—with the cartilaginous substance, since madder (*rubia tinctorum*), which has a strong affinity for phosphate of lime, but none for lime or calcium, is attracted, during the process of nutrition, by the bones from the blood of an animal fed upon it; and, moreover, several acids decompose the salt of lime contained in the bones, and extract it without altering the form or composition of the cartilaginous framework.*

Excluding from consideration the substances which in individual cases may be educt or product of chemical analysis, we may with Professor Weber regard those matters, which appear to be mixed in the animal body with the more essential proximate principles, as divisible in two classes.

The first class may consist of binary compounds of mineral substances only; such as phosphate of soda, phosphate of lime, phosphate of magnesia, carbonate of soda, carbonate of lime, muriate of potash, muriate of soda, fluoride of calcium, silica, oxide of manganese, oxide of iron, and soda.

In the second class are included binary compounds of organic with mineral or inorganic substances; such as the compound which the albumen is supposed to form with soda in the blood—albuminate of soda—and the salts of lactic acid—lactates of potash and soda.

The simplest forms in which organic matter appears, have now to be considered.

The first form is that of complete solution. There are many fluids containing organic matter, in which no visible molecules can be discovered; such, for instance, is the serum of blood, until it is subjected to the influence of heat, galvanism, or different chemical agents. A part of the animal matter of the lymph and chyle is also in the state of solution.

The second form is the state of softness which the solid organised tissues present, and which is peculiar to organic beings. The tissues derive their properties of extensibility and flexibility from the water, which constitutes four-fifths of their weight; although they cannot be said to be wet, and do not impart their water to other substances so as to moisten them. This water appears, as Berzelius remarks, not to be chemically combined in them; for it is gradually given off by evaporation, and can be extracted at once by strong pressure between blotting-paper. When deprived of its water, animal matter becomes wholly insusceptible of vitality; except in the case of some of the lower animals, which, as well as some plants, revive when again moistened.†

* Weber, loc. cit. p. 318, 340.

† Berzelius, Thierchemie, p. 7.

According to Chevreul, pure water alone can reduce organised substances to this state of softness; although salt water, alcohol, ether, and oil are also imbibed by dry animal textures. Moist animal tissues, by virtue of their porosity, allow soluble matters, which come into contact with them, to be dissolved by the water which they contain, and which fills their pores; if the matters are already in solution, they are imparted by their solutions to the water of the tissues. Gaseous substances are taken up in the same way. Matters, also, which are contained in solution in one tissue, are rapidly imparted to other tissues which can dissolve them. The laws of the attraction of substances in solution and mixture, the laws governing the uniform distribution of miscible fluids, are therefore also applicable in the case of moist animal tissues.*

Organic substances are during life never crystallized, and the excreted matters of animals which are crystallizable, viz. urea, lithic acid, and some fatty matters, are never found crystallized in the living tissues, although crystallized mineral substances are sometimes observed in the cells of plants.

The organic matter frequently appears in the form of microscopic molecules. These organic molecules are observed partly in fluids: such are the red particles of the blood which in man measure from $\frac{1}{3700}$ to $\frac{1}{4600}$ of an inch, the globules of the chyle which measure $\frac{1}{7190}$ of an inch according to Prevost and Dumas, and those of the saliva, which measure $\frac{1}{2770}$ of an inch, according to Weber. The globules of coagulated albumen and fibrin are less distinct. Many even of the tissues of organised bodies, particularly of animals, appear to consist of molecules aggregated in the form of fibres, lamellæ, and membranes. These molecules are most distinct in the brain, and in the embryo, for instance, in the germinal membrane of the ovum; in other tissues, it is by no means certain that the appearance of molecules, observed under the microscope, is not an illusion produced merely by inequalities of the surface. The opaque part of the germinal membrane in the ovum of the bird is evidently composed of globules of considerable size, which are visible with a simple lens and are perfectly similar to the globules of the yolk: but the vessels which are already distributed through the germinal membrane are, according to my observations, formed of an incomparably finer matter; as are also the central transparent part of the germinal membrane, the area pellucida, and the embryo itself. It appears, indeed, that the germinal membrane is formed by the attraction and aggregation of the globules of the yolk; but all the parts developed in this germinal membrane are produced by solution of these globules, and conversion of them into a matter in which no elementary particles can be distinctly recognised, and of which the molecules must at any rate be beyond comparison more minute than the globules of the yolk and germinal membrane.

* See the observations on imbibition in the section on Absorption by the capillaries.

The ultimate muscular fibre in the frog is five or eight times more minute than the red particles of its blood, and more minute even than the nuclei of these red particles; the thickness of the muscular fibre in the frog and in mammalia is nearly the same, while the size of the red particles of the blood in the two is very different. The diameter of the ultimate nervous fibre in mammalia is, according to my observation, twice or three times less than that of their blood corpuscules, and is greater than that of the nuclei of the blood corpuscules. In the frog, the primitive nervous fibre has only $\frac{1}{8}$th the diameter of its blood corpuscules, and is therefore much smaller than the nucleus of the blood corpuscule. I have not been able to satisfy myself that the nervous fibrils consist of globules arranged in a linear form. They certainly present successive inequalities, but these inequalities are not regular. In fine, this theory of the composition of tissues by the aggregation of globules, which are supposed to be more than $\frac{1}{2000}$ of a line in diameter, is rendered exceedingly improbable by the discovery of Ehrenberg, that monads, which themselves do not measure more than $\frac{1}{2000}$ of a line, have compound organs. On account of the difficulty of distinguishing by the microscope between inequalities and globules, this theory still remains a mere hypothesis. At any rate, the organic molecules are merely the most minute forms in which the compound organic matter appears; they are not the atoms of the organic combination.

Source of organic matter.—It is only in organic bodies themselves, that the peculiar force which animates them is observed. It is manifested only in the organic compounds produced in these bodies; the mere accidental coming together of the elementary components is not capable of producing organic matter. Fray, it is true, asserts that he has observed the formation of microscopic infusoria in pure water; and Gruithuisen says, that he has seen a gelatinous membrane form in infusions of granite, chalk, and marble, and infusory animalcules subsequently appear in this membrane. The fact observed by Retzius* is also remarkable; namely, that a peculiar kind of conferva was generated in a solution of muriate of barytes in distilled water, which had been kept half a year in a bottle closed with a glass stopper. But, in these remarkable cases, it is certain that either the vessels, or the water, contained organic matter, in however small quantity; and, according to the experiments of Schultze, the most minute particles of organic matter are sufficient under favourable circumstances to produce the phenomena which have been regarded as instances of equivocal generation.

Even animals themselves have not the power of generating organic matter out of simple inorganic elements or binary compounds; they grow by the assumption of matter already organised, whether animal or vegetable; they have the power of preserving organic compounds and of converting one into another, but they cannot produce them. Plants, on

* Froriep's Notizen, v. p. 56.

the contrary, seem to be able not merely to assimilate the organic matter of animals and plants, but also to generate them from simple elementary bodies and compounds of these, such as carbonic acid and water, although the presence of some organic matter in the soil, in which plants grow, is necessary. It seems impossible to deny this production of organic matter from inorganic matter by plants; for, unless such were the case, the nutriment on the earth would be constantly decreasing, since animal and vegetable matters are being incessantly converted by combustion, putrefaction, &c. into binary compounds.

The organic matter formed by plants, or that contained in plants and animals and modified by them, is capable of again forming a part of other living beings, when taken into them and subjected to their vital forces. In this manner all the organic matter which is spread over the surface of the earth, originates in living beings: death, that is, the extinction of the power which produces and maintains organic compounds, annihilates the individual; while the organic matter which formed this individual, while it is not reduced to binary compounds, is still capable of receiving new life, or, in other words, of nourishing other living bodies.

remark:
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Equivocal generation.—The ordinary mode of production of organic beings is from others of the same species, by ova or shoots. But it must be inquired, whether the organic matter left after the destruction of one living body can, under certain circumstances, generate living bodies of another kind; whether it is capable, not only of nourishing bodies already living, but also of continuing its own life in a modified form; whether, in fact, under certain conditions,—namely, under the influence of atmospheric air, water, and light,—small microscopic animals, the infusoria, and under other conditions the simplest plants, forming mould, are generated from this apparently dead organic matter.

In a more extended sense the ancients, especially Aristotle, had admitted this equivocal generation, this spontaneous formation of animals; for they had an old tradition, that the lower animals, insects and worms, were generated during putrefaction. This opinion was still maintained among the other superstitions of natural history and medicine even in the seventeenth century. At that period Redi wrote his "Experimenta circa generationem insectorum," in which he proved that all the instances of equivocal generation, which the ancients had adduced, were erroneous; that all these worms and insects were produced from ova which had been previously deposited. His proofs were convincing, and from that time no well-informed naturalist believed in the fable of generation by putrefaction; so that the proverb "Omne vivum ex ovo," retained its force. Subsequently, however, Needham* pointed out, that although no insects are produced by putrefaction, yet that, during that process, minute microscopic animals till then unknown are generated. If water is poured over animal or

* Nouv. Observ. Microscop. and "New Microscopic Discoveries," London 1745.

vegetable substances, and the infusion exposed to air and light at the usual temperature of summer, after a few days the organic matter will have undergone partial decomposition, being in part converted into other organic matters, partly reduced to globules, and in part dissolved; and there will appear in it either mould, or those microscopic animals, in which Ehrenberg has discovered a very complicated organisation.

Since the time of Needham, our knowledge of this subject has been extended by the observations of Wrisberg, O. F. Müller, Ingenhouss, G. R. Treviranus, Gruithuisen, and Schultze.

Wrisberg* observed, that no animalcules are produced when atmospheric air is excluded, for instance, when the surface of the infusion is covered with olive oil. They are generated by an infusion of any animal or vegetable matter which contains nothing acrid or acid, and nothing which would prevent putrefaction. The development of infusoria commences as soon as a certain degree of decomposition with escape of gas has taken place. From this time a large number of microscopic molecules are seen in the infusion; these molecules are sometimes diffused in it, sometimes form a kind of membrane at its surface, and are produced by the dissolution of the organic matter. Fray and Burdach† state, that infusory animalcules are also generated in an atmosphere of hydrogen and nitrogen.

Spallanzani and several other physiologists attacked this theory of the equivocal generation of animalcules. Spallanzani‡ explained the production of these animals by supposing ova to have been present in the fluid, and to be developed by the influence of warmth, water, air, and light. This physiologist's own experiments, however, show that organic substances do not lose their property of producing animalcules by being boiled, and that distilled water is as well adapted for making the infusion as other water. Besides, Spallanzani's experiments merely prove that atmospheric air is necessary for the development of these animalcules; and that, when bottles filled with infusions, and hermetically closed, were exposed for an hour to boiling heat in vessels filled with water, no animalcules were afterwards discoverable in these infusions. Spallanzani also found that the animalcules differ according to the nature of the infusion. From experiments with the seeds of the water-melon, gourd, hemp, and millet, it resulted that the number of the infusoria is greater when the germ is in the progress of growth, than when the seed is just germinating, and that the number diminishes as the seed decays. The smaller kinds of animalcules were succeeded by larger, until, after a certain time, the power of developing them seemed to be lost. The infusory animalcules from uninjured seeds were said to be larger than those from pulverized seeds. They were generated from flour quite as well as from seeds merely bruised. If, however, the starch of the flour was separated from the

* Observ. de Anim. Infus.

† Burdach, Physiologie, t. i.

‡ Physical. und Mathem. Abhandl.

gluten, and an infusion made of each of these substances separately, very few animalcules, or none at all, were developed in the infusion of starch, while in that of the gluten a host of living animals were seen. In infusions of barley, Indian wheat, beans, lupin-seeds, rice, and linseed, no animalcules were developed.* But since the genera and species of infusoria are as determinate as those of higher classes of animals, and since Spallanzani has not particularized the differences of form of his infusoria, since moreover the forms of the infusoria in the different stages of their development are not known, Spallanzani's experiments lose much of their weight in reference to his discovery of perfectly different animalcules in the infusions of the gourd, chamomile, sorrel, corn, and spelt.

Treviranus† has, by his numerous and more accurate experiments, given a much greater importance to the hypothesis of equivocal generation. The following are the grounds of his arguments:

1. Infusions, with the same water, of different organic substances,—for instance, cress-seeds and rye,—give rise to different animalcules.

2. Light has a very great influence on the process of equivocal generation. Thus, the green matter of Priestley, which is remarkable for its property of exhaling oxygen, is produced only under the influence of light; when water, particularly spring-water, is exposed to the sun in transparent vessels, whether open or close, this matter appears in the form of a greenish crust consisting of round or elliptic granules, in which crust at first the slight motions of single molecules are discovered, and afterwards transparent threads moving irregularly. These changes have been most fully observed by Ingenhouss.‡ According to Professor R. Wagner, the green matter of Priestley consists of the remains of green animalcules, the euglena viridis and others, which have died. In that case the moving threads would be independent beings, distinct from the green matter, and Ingenhouss would have committed the error of regarding different kinds of simple beings as different states of the same molecules.

3. The entozoa and the spermatozoa, bodies with tails and spontaneous motions, which are seen by the microscope in the seminal fluid, even of invertebrate animals, seem to afford arguments for the spontaneous origin of living beings in organic matter.

4. Treviranus found in his own experiments that, under circumstances otherwise similar, different organic beings, namely infusoria or mould, are formed in different infusions; and he found that these differences did not depend on the water, but on the substances infused in it.

5. Treviranus observed that in one and the same infusion, under different accidental conditions, different animalcules were developed; thus, from an infusion of the leaves of the iris with fresh spring-water, in a long vessel covered with linen, and exposed to the sun, infusory ani-

* Treviranus, Biologie, ii. pp. 279, 280. † Biologie, ii. p. 264—406.

‡ Vermischte Schriften phys. medic. Inhalts.

malcules were generated; in another vessel, placed in another situation, the green matter of Priestley was formed. Thus also the products in the same infusion of rye with spring-water were different, when Treviranus placed a bar of iron in one of the vessels. This result seems to agree with that of Gleditsch, who found that in separate portions of melon covered with muslin, and placed at different heights, the various living organic substances, namely mould, byssus, and tremellæ, were produced in different proportions. To this might be added, that Gruithuisen states that he has found perfectly different animalcules in infusions of pus and mucus.

From all these facts Treviranus has inferred, that throughout all nature there exists an absolutely indecomposible, indestructible (?) organic matter which is constantly active; which gives life to every thing living, from the byssus to the palm, and from the point-like infusory animalcule to the monsters of the deep; and which, in its essence unchangeable, is constantly changing its form: that this matter has itself no proper form, but is capable of assuming every form of life; that it receives a determinate form only under the influence of external causes, retains this form only during the continuance of these causes, and takes another form as soon as other causes act upon it. According to Wrisberg and others, the animalcules are formed from particles which separate from the substance infused, and which gradually begin to move; while Gruithuisen* says, that they appear first in the solution of extractive matter obtained by the action of the water on the infused substance. Professor Schultze † says, "I have never seen a globule of blood, or of milk, or of cerebral substance, begin to move about in their several infusions, as a monad, or become changed into one. Every single globule, by its solution, affords matter for the production of several hundred monads." This last observation, however, does not agree with the results of measurement; for Ehrenberg estimates the smallest visible monad at about $\frac{1}{2000}$ of a line, that is $\frac{1}{24000}$ of an inch; while the corpuscules of human blood are only $\frac{1}{3700}$ — $\frac{1}{4600}$ of an inch in diameter, and the globules of the milk are still smaller. Schultze states that he has observed the conversion of dust-like particles of organic matter into infusoria; these particles in the water become, he says, in a few hours surrounded by a turbid ring which extends until the particle is quite dissolved; this ring separates into monads.

Equivocal generation not proved by these observations.—If we criticise the observations of these observers, we shall find that the mode in which the experiments have been performed do not leave the results free from doubt.

1. In the experiments made with boiled organic matter, in the air, it is not certain that the infusoria or mould did not arise from the dust of

* Gruithuisen, Beiträge zur Physiognosie und Eautognosie. München, 1812. 8vo.

† C. A. S. Schultze, Microscop. Untersuchungen über R. Brown's Entdeckung lebend. Theilchen in allen Körpern, und über Erzeugung der Monaden. Carlsruhe, 1824.

desiccated animalcules, or their germs, floating in the air. Perhaps, as Humboldt remarks,* when waters on the surface are dried up, the winds take up the germs of the simplest organic beings, which, being received by other water in the form of dust, are revivified, as in the well known and attested fact of the revivification of the wheel-animalcule, first observed by Spallanzani. The fact of the dust which floats throughout the air containing particles which swell when moistened, has very recently been applied by Schultze to explain the production of infusoria; he regards these particles as monads which have been dried, and which when moistened recover life. Schultze, however, does not consider this very frequent source of infusoria as the only one; he admits the conversion of organic substance into protozoa.

2. The equivocal generation of infusoria is not better proved by the experiments in which boiled organic substances and common water were used; for the water may have contained the ova of infusoria, or animalcules themselves, which have afterwards multiplied very rapidly at the expense of the organic matter in the infusion. The use of perfectly pure distilled water can scarcely be presupposed, for even water distilled five times may still contain organic particles.

3. Those who have experimented with fresh organic substances and distilled water, or even artificially prepared gases, cannot prove that the ova of animalcules, or animalcules themselves, were not in some way contained in the organic substance: the microscopic animalcules which are known to exist in living tissues are indeed few, and the common globules of the organic fluids, such as those of the blood, have certainly no individual life; but mucus itself contains microscopic animals; the intestinal mucus of the frog, as well as the semen, contains animalcules. Baer has seen microscopic particles moving spontaneously at different spots in the muscles.† The grain of wheat, and some varieties of agrostis, often contain vibriones, which even after being dried recover their active life if moistened. Some animalcules also which are met with in other animals, but especially the epizoa, will continue to live when placed in water.

4. Lastly, although some experimenters should have employed organic substances long boiled, with distilled water and artificially prepared air at the same time, still the accuracy necessary for a sure result is neither probable nor generally possible, since every instrument used for changing the water ought to be absolutely free from particles of organic matter, and every cleansing is a source of errors.

Ehrenberg's observations are opposed to the theory.—These remarks do not disprove the existence of the equivocal generation; they merely show that it is scarcely possible to prove it by direct experiment. The investigations of Ehrenberg, however, relative to the organisation of these

* In his Ansichten der Natur.

† See Nov. Act. Nat. Cur. 13. 2. p. 594.

animals and plants, which are supposed to be generated in this equivocal manner, have thrown new doubt upon the theory. In the first place Ehrenberg discovered the real germs of the fungi and mould.* The propagation of these organic bodies was thus established; it was shown that, by means of the germs or seeds of the mould, new mould can be produced, which rendered it probable that the cases of the unexpected production of mould arose merely from seeds, which had been diffused in the atmosphere or water, having then found the situation required for their development. With regard to the infusory animalcules, their complicated structure was first discovered by Ehrenberg; he found that the smallest monad $\frac{1}{2000}$ of a line in diameter has a complicated stomach, and organs of motion, in the form of cilia. In others he observed the ova, and the propagation by ova. This excited the greatest doubt with regard to those earlier observations, in which, the complicated structure of these animalcules being unknown, they were said to have been seen to originate in particles of the organic substance of the infusion. Ehrenberg has never succeeded in obtaining determinate forms of infusoria, according to the nature of the infusion; and even by the most similar modes of performing the experiment, sometimes one, sometimes another set of animalcules were obtained. Ehrenberg believes that there are certain forms, of which the number is limited, which are most widely diffused; the ova or individuals of these forms may exist in all waters, even in some parts of plants, but perhaps only in the noxious parts; and of these forms different kinds may be much multiplied, according to the kinds of ova or individuals which were in the water, or were introduced into it. The increase of these animals appears to be extraordinarily rapid. A single wheel-animalcule, Hydatina Senta, which was watched for more than eighteen days, and which lives still longer, is capable of a four-fold increase in twenty-four or thirty hours. This rate of increase affords in ten days a million of beings. This, in some measure, explains the extraordinary number of infusoria in a drop of an infusion. Ehrenberg never observed any animalcules in dew or rain; but he has found some in Africa and Asia as well as in Europe, in sea water as well as in river water, in the depths of the earth and at its surface. During their development, however, these animals seem to present many forms, and the forms dependent on the different stages of development of one animalcule may be easily mistaken for examples of different species. From these observations Ehrenberg concludes, that all infusoria are, like other animals, propagated from ova,—omne vivum ex ovo,—and leaves it undecided whether the ova are, or are not, in part really the product of a generatio primitiva.†

* Nov. Act. Nat. Cur. t. x. See also Ness. v. Esenbeck, Flora, 1826, p. 531; and Schilling in Kastner's Archiv. x. p. 429.

† Ehrenberg in Poggendorf's Annal. 1832. 1. See also Wagner in the Isis for 1832. Wagner regards as certain, the transformation of infusoria into the green

How is this to my theory — & parasitic insects)

Facts relating to Entozoa, favourable to equivocal generation.—The primitive formation of certain animals from animal matter, till then unorganised, is still best supported by the facts regarding the entozoa. A complete series of arguments in favour of equivocal generation rests upon the impossibility of explaining the first production of entozoa, without supposing a spontaneous generation. 1. The immense majority of the intestinal worms are quite distinct in their organisation from all the beings which are met with out of the animal body. The similarity of some distomata to the planariæ of fresh and salt water is only apparent. 2. A small number only of intestinal worms occur in different genera of animals. Thus the Tænia of man is peculiar to him; on the contrary, the Distoma Hepaticum, the hydatid of the liver, seems to be common to man, the hare, cow, camel, deer, horse, and hog; the thread-worm, Ascaris Lumbricoides, is common to man, the hog, ox, and horse. Most animals have their peculiar intestinal worms, differing specifically from those of others. 3. Many of these entozoa occur only in particular organs. 4. Intestinal worms generally die when removed from the animal body. 5. They have been observed even in the embryo. 6. The fact of animals, which feed on vegetables solely, having nevertheless their own peculiar entozoa, proves that these entozoa, or their germs, cannot be introduced with the food. In carnivorous animals this introduction of the entozoa from without can be admitted in very few cases only; such are the facts of the Echinorhynchus of the field-mouse having been sometimes found in the falcon, the worms of the frog in serpents, the Ligula of fishes, the Bothriocephalus solidus of the stickleback, in the intestines of wading and swimming birds. But many other entozoa are met with in other parts than the intestinal canal, and beyond the reach of matters introduced from without.*

like diseases proof of relation of man to other animals

great energy

Ehrenberg endeavours to set aside the equivocal generation of the entozoa, inclining to the old opinion that the ova of these animals circulate with the fluids in all parts of the body. He assumes that, since the generative organs of the entozoa contain a great number of ova, these ova are carried by the circulation into all parts of the body; so that all the fluids are, as it were, infected with the ova of the entozoa, which are seated in particular organs. The milk with which other individuals of the same species are nourished, may itself contain the ova of these worms. The embryo of mammalia in which entozoa already exist, may receive the ova from the fluids of the mother. Entozoa have been found in the eggs of birds. Eschscholz found them in hen's eggs.† It

matter of Priestley, as many persons have described. This green matter, however, is nothing more than the remains of dead infusoria, the euglena viridis. The conversion of this green matter into confervæ, ulvæ, tremellæ, or even mosses, is doubted by Wagner, and with justice.

* Bremser, Ueber lebenden Würmer im lebenden Menschen. Wien, 1819.

† Burdach's Physiologie, i. p. 22.

is possible that they may have originally found their way thither from the fluids of the mother; but, in fact, the suppositions on which the equivocal generation is here sought to be refuted, are as improbable as that theory itself. The ova of the entozoa are evidently too large to enter the lymphatics of the organ in which the worms live; they are much too large to circulate in capillary blood-vessels, of which the diameter is only $\frac{1}{4000}$ of an inch, or in fine to pass into the secretions,—the milk, or yolk of the egg, for example: the explanation of the occurrence of entozoa in herbivorous animals, by transmission from mother to young, is consequently completely opposed to the known data afforded by the micrometer, unless it be admitted, that the smallest particle of the germinal matter formed by entozoa already existing is as capable of propagating them as an entire ovum. With regard to the spermatozoa, Ehrenberg assumes that every animal receives them at the time of fecundation.

M. Von Baer * has observed many other extraordinary circumstances in the generation of the entozoa. The animals which he names Bucephalus, are generated in thread-like ovistocks, which are found in muscles; and Bojanus and Baer have described a worm, found in the lymnæus stagnalis, which again contains numerous animals of a perfectly different form,—the cercaria. Nordmann† has seen monads in the body of living intestinal worms, namely, diplostomata; and has seen infusory animalcules produced in the interior of the putrefying ova of lernææ. On the other hand, the changes which certain entozoa undergo deserve attention; for example, the ligula and bothriocephalus solidus of fishes have no distinct genital organs until they are received into the intestines of water birds: some young distomata have at first a different form from that which they afterwards present; thus the distoma nodulosum of the perch has, according to Nordmann, at first no sucker, and is, then, provided with a trace of an eye and with cilia, as if to swim in water. The infusoria and entozoa of living plants still require investigation. It is important to know, that the diseased grain of agrostis or bent-grass, phalaris or canary-grass, and wheat, contain, according to Steinbuch‡ and Bauer,§ vibriones; that Bauer, having inserted vibriones into the stem of the young wheat, found them again in the grain; and that the worms of the dried seeds, according to the same observers, if placed in water after several years, will again present all the phenomena of life.

Origin of organic matter and of the organic force.—In the production of infusoria there is no new formation of organic matter; the previous existence of organic beings is presupposed. Organic matter is never produced spontaneously. Plants alone seem to have the power of generating ternary or organic compounds from binary or inorganic compounds; while animals are nourished only by organic matter, which

* Nov. Act. Cur. XIII. 2. † Microgr. Beitrage. Berlin, 1832.
‡ Analecten. 1802. § Philos. Trans. 1823.

they cannot generate from binary compounds, and consequently their existence presupposes that of the vegetable kingdom. How organic beings were originally produced, and how organic matter became endowed with a force which is absolutely necessary to the formation and preservation of this organic matter, but which is manifested only in it, it is beyond the compass of our experience and knowledge to determine. The difficulty is not removed by saying that the organic force has resided in the organic matter from eternity, as if organic force and organic matter were only different ways of regarding the same object: for, in fact, the organic phenomena are presented only by a certain combination of the elements; and even organic matter, itself susceptible of life, is reduced to inorganic compounds as soon as the cause of the vital phenomena, namely, the vital force, ceases to exist. This problem, however, is not a subject of experimental physiology, but of philosophy. Conviction in philosophy and in natural science has entirely different bases; the first suggestion here, therefore, is, not to be led away from the field of rational experiment. We must be content to know that the forces which give life to organic bodies are peculiar, and then examine more closely their properties.

2. *Of Organism and Life.*

Organised beings are composed of a number of essential and mutually dependent parts.—The manner in which their elements are combined is not the only difference between organic and inorganic bodies; there is in living organic matter a principle constantly in action, the operations of which are in accordance with a rational plan, so that the individual parts, which it creates in the body, are adapted to the design of the whole; and this it is which distinguishes organism. Kant says, "The cause of the particular mode of existence of each part of a living body resides in the whole, while in dead masses each part contains this cause within itself." This explains why a mere part separated from an organised whole generally does not continue to live; why, in fact, an organised body appears to be one and indivisible. And since the different parts of an organised body are heterogeneous members of one whole, and essential to its perfect state, the trunk cannot live after the loss of one of these parts.

It is only in very simple animals or plants which possess a certain number of similar parts, or when the dissimilar parts are repeated in each successive segment of the individual, that the body can be divided, and the two portions, still possessing all the essential parts of the whole, though in smaller number, continue to live. Branches of plants separated from the trunk, being planted, form new individuals. The different parts of plants are so similar, that they are convertible one

into another, branches into roots, and stamens into petals.* This is the case also with some simple polypes. The experiments of Trembley, Roesel, and others, prove that portions of a divided polype will continue to grow until each half becomes a perfect animal. In the same way some worms, as the naides, in which each segment contains nearly the same essential parts,—the intestine, nerves, and blood-vessels,—have been observed to propagate by spontaneous division. Bonnet states, that he has seen this new growth and reproduction in the portions of a divided earthworm; but this animal, when thus divided, could not continue to live, for neither portion would contain all the parts essential to the whole. Yet a snail will reproduce its head! –

In the higher animals, and in man, there are certain organs,—that is, parts differing in their properties and functions,—which cannot be removed without destruction of life, and of our idea of the whole; and such organs also only occur singly, as brain, spinal marrow, lungs, heart, and intestinal canal. Other parts, on the contrary, which are not members essentially necessary to our conceived idea of the whole, or which are several in number, may be removed with impunity: no part, however, of one of the higher animals can continue to live when separated from the body, for no one part contains all the organs essential to the whole. The ovum, the germ itself, alone possesses this power; for, at the time of its separation from the parent animal, the vital force has not formed in the germ the essential parts of the whole; and yet, when separated from the original being, it forms a new integral being. There is then in the organism a unity of the whole, which governs its formation out of dissimilar parts. From the facts we have stated, however, it appears that organised bodies are not absolutely indivisible; they may indeed always be divided, and still retain their properties, if each portion contains the essential heterogeneous members of the whole, and in the generation even of the highest animals and plants a division takes place.

There must be some wide difference between ovum & bud: –

The parts of inorganic bodies are homogeneous and independent of each other.—Inorganic bodies are divisible in a much more extended sense, without the parts losing the chemical properties of the whole: they may be divided (to use the common expression) *ad infinitum*,—that is, according to the atomic theory, into the ultimate atoms which, on account of their minuteness, elude the senses; and in chemical compounds into molecules which are formed of the different component atoms, and which are likewise not recognisable by the senses.

There are, however, even among inorganic bodies, some which cannot be reduced by division to their ultimate particles without losing some of their properties; I mean the crystals. These bodies can be divided with facility only in certain directions, and the portions thus ob-

* Goethe, Metamorphose der Pflanzen.

There must be in the bisected parts organs sufficient to keep them alive. or they any part may be reproduced. –

tained are often different in form from the whole; for which reason some persons regard crystals also as "individuals," which exist from the continuance of the force which formed them, and cease to exist when external, chemical (atmospheric), or mechanical influences overcome their force of crystallisation or hardness.* But even if crystals are regarded as individuals in this sense, there is still this great distinction between them and organised bodies,—that the molecules of crystals are homogeneous throughout, and that crystals are divisible, at least, into homogeneous aggregates; while organised bodies are composed of perfectly different members of one whole, such as tissues endowed with peculiar properties. Organic combinations, moreover, never occur in a state of crystallisation in organised bodies during life. Again, in an inorganic body which is composed of heterogeneous substances aggregated together, these parts have no reference to the design and existence of the whole.

Adaptation displayed in organised bodies. — Organised bodies being composed of a certain number of dissimilar essential parts all adapted to the plan of the whole, it necessarily follows that the external and internal conformation of themselves and of their organs are such as to distinguish them entirely from inorganic bodies. That which we admire in the whole animal is not merely the manifestation of the ruling forces, as crystallisation is the consequence and manifestation of a certain force in a binary compound; but the form of the animals and of their organs evidences also an arrangement rationally adapted to the exercise of the forces, a most excellent harmony of the organisation with the faculties intended to be exercised. Crystals, on the contrary, present no adaptation of form to an intended action of the whole, because the whole crystal is not a body composed of a number of dissimilar adapted tissues, but is produced merely by the aggregation of similar elements or formative particles, all subject to the same laws of crystalline attraction. Crystals, therefore, increase by the aggregation of new particles on the external surface of the parts already formed; while in the organised body the formation of the parts situated side by side, each having a different organisation, is for the most part contemporaneous; so that the growth of organised bodies takes place in all particles of their substance at the same time, while the increase of the mass in inorganic bodies is produced by external apposition.†

(as the effect of (~~every~~) circumstances

This law of organic conformation,—adaptation to ~~an end~~, — regulates the form, not only of entire organs, but also of the simplest elementary tissues. Thus it will in a future page be shown, that the manifold

* See Mohs, Grundriss der Mineralogie, i. Vorrede, p. 6.

† Professor E. H. Weber has made some other very interesting comparisons between organisation and crystallisation in his General Anatomy. Hildebrandt's Anat. 1ster Band.

forms of secreting glandular structures depend simply on the various modes in which a large secreting surface can be realised in a small space. The fibrous structure of muscles is necessary to enable these organs to shorten themselves in a determined direction by the zigzag flexure of the fibres. Thus also in treating of the Physiology of the Nerves it will be shown, that unless the nerves had been divided into a certain number of primitive fibres, which do not communicate one with another, their local action,—local circumscribed sensation,—would be impossible. The same adaptation is seen to be equally necessary in the organisation of plants. The organs of plants are less heterogeneous, and, in place of being so much enclosed in the interior, are expanded on the surface,—the reciprocal actions with the external world being effected by the whole surface rather than by particular points; hence the general character of the conformation of plants is a surface increasing in perfect conformity with the intended purpose, this surface being presented in the manifold forms of the leaves; the individual forms in which the increase of surface is effected are more numerous than the most lively fancy can imagine, and a great part of terminology is only an attempt to form logically, a plan conformable to nature, of the possible varieties in the increase of surface obtained by variations of the leaves, and of their relation to pedicle, twig, branch, and stem.

Organic symmetry as distinguished from inorganic.—The only character that can be possibly compared in organic and inorganic bodies, is the mode in which symmetry is realised in each. Crystals have symmetrical and asymmetrical surfaces, angles and corners. Animals have also symmetrical and asymmetrical parts, and the laws of symmetrical and asymmetrical conformation in organised bodies present similar manifold variations. The original form of the animal germ, for example, is a roundish flat disk,—the cicatricula (germinal disk, blastoderma) in the bird's egg; this germinal disk, while in the ovary, appears, from the researches of Purkinje and Baer, to be a vesicle. The germ is also disk-shaped in invertebrate animals, as I have seen in the planaria. The form of the ovum and yolk must not be confounded with that of the germ. The forms developed from the germ, however, are very various. For instance, we recognise first a radiate symmetrical type in the radiata, similar parts being arranged around a common point; the anterior and posterior surfaces of the body being the only asymmetrical parts. Secondly, we distinguish the symmetry of similar parts in an arborescent type, as presented by the leaves and flowers in plants, and by the polypes on the branched stem in polypiferous animals. Thirdly, we distinguish the successive symmetry in the succession of similar parts from before backwards in worms, in which the only want of symmetry is between the dorsal and ventral surfaces. Fourthly and lastly, we recognise the lateral symmetry in the repetition of similar parts on each side, in man and the higher

animals; here the want of symmetry is seen in the organs taken from before backwards, and in the dissimilarity of the dorsal and ventral surfaces. In many animals the lateral symmetry is in part combined with the successive symmetry, which is seen in the vertebræ of the higher animals. In addition to the circumstance that the symmetry and asymmetry of crystallised inorganic bodies are always represented by plane surfaces and straight lines, the reverse of which is the case in organised bodies, there is also this great difference, that the symmetrical and asymmetrical parts of crystals have a simple composition, while the symmetrical parts of organised bodies are themselves in the first place formed of heterogeneous tissues. The causes which give rise to the different types of organic symmetry, just mentioned, and which first determine in the germ the position of the axis for the symmetrical developement, are as difficult to imagine as the causes of the symmetry of form in crystals.

The *elementary particles of the organised body are, moreover, never crystalline;* for although some kinds of fatty matter are crystalline in the pure state, it is only when they are subjected to external influences and withdrawn from that of life. The same is the case with sugar, urea, and lithic acid. Most of the organic substances and fluids do not crystallise even when removed from the living body. The spinal canal and the cranial cavity of the frog have, surrounding the central parts of the nervous system, a layer of white pulpy matter which, according to Ehrenberg and Huschke, consists of microscopic crystals of carbonate of lime. In the peritoneum of fishes, and in the tapetum of the choroid of the same animals, Ehrenberg* has also discovered microscopic crystals of organic matter.

[Professor Schoenlein † has discovered, in the intestinal excretions, and in the yellow crusts covering the excrescences of the mucous membrane in typhus abdominalis, which are supposed to be Peyer's follicles, a great number of small crystals, which consist chiefly of phosphate of lime, some sulphate of lime, and a salt of soda. In other kinds of fevers and of diarrhœa, and in healthy persons, the fæces contained no crystals.

Dr. Valentin‡ has observed an imperfect crystallisation of the calcareous matter which forms the shell of the egg of the lacerta viridis.]

The organic force is also creative.—Hitherto I have examined merely that peculiarity of organised bodies which consists in their being systems of dissimilar organs, the existence of each of which has its source, not in itself, but in the entire system, as Kant expressed it. *The organic force,* which resides in the whole, and on which the existence of each part depends, has however also the property of generating from organic matter the individual organs necessary to the whole. Some have believed that life,—the active phenomena of organised bodies,—is only the result of

* Müller's Archiv. für Anat. und Physiolog. 1834, p. 158.

† Ibid. 1836, p. 258. ‡ Ibid. p. 256.

the harmony of the different parts—of the mutual action, as it were, of the wheels of the machine,—and that death is the consequence of a disturbance of this harmony. This reciprocal action of parts on each other, evidently exists; for respiration in the lungs is the cause of the activity of the heart, and the motion of the heart at every moment sends blood, prepared by respiration, to the brain, which thus acquires the power of animating all other organs, and again gives occasion to the respiratory movements. The external impulse to the whole machinery is the atmospheric air in respiration. Any injury to one of the principal moving powers in the mechanism, every considerable lesion of the lungs, heart, or brain, may be the cause of death; hence these organs have been named the *atria mortis.* But the harmonious action of the essential parts of the individual subsists only by the influence of a force, the operation of which is extended to all parts of the body, and which does not depend on any single parts; this force exists before the harmonizing parts, which are, in fact, formed by it during the developement of the embryo. A complicated piece of machinery, constructed in adaptation to an end,—for example, a watch,—may present an action resulting from the co-operation of individual parts, and originating in one cause: but organic beings do not merely subsist by virtue of an accidental combination of elements; the vital force inherent in them itself generates from organic matter the essential organs which constitute the whole being. This rational creative force is exerted in every animal strictly in accordance with what the nature of each requires.

The creative force exists already in the germ, and creates in it the essential parts of the future animal.—The germ is "potentially" the whole animal; during the developement of the germ, the essential parts which constitute the "actual" whole are produced. The developement of the separate parts out of the simple mass is observable in the incubated egg. All the parts of the egg, except the germinal membrane or blastoderma, are destined for the nutrition of the germ; the entire vital principle of the egg resides in the germinal disk alone, and since the external influences which act on the germs of the most different organic beings are the same, we must regard the simple germinal disk, consisting of granular amorphous matter, as the "potential" whole of the future animal, endowed with the essential and specific force or principle of the future being, and capable of increasing the very small amount of this specific force and matter which it already possesses, by the assimilation of new matter. The germ expands to form the germinal membrane, which grows so as to surround the yolk; and by transformation of this germ the organs of the future animal are produced, the elements merely of the nervous and vascular systems, and of the intestinal canal, being first formed, and from these elements the details of the organisation afterwards more fully developed; so that the first trace of the central parts of the nervous system

now in a bud. we must suppose there is one
particle of old organized structure. — a filament of nerve,

must be regarded neither as brain nor as spinal marrow, but as the still "potential" whole of the central parts of the nervous system. In the same manner the different parts of the heart are seen to be developed from a uniform tube; and the first trace of the intestinal tube when there are no salivary glands and liver, is more than the mere intestinal tube; it is the "potential" whole,—the representative of the entire digestive apparatus; for, as Baer first discovered, liver, salivary glands, and pancreas are in the further progress of the vegetative process really developed from that which appears to be merely the rudiment of the intestinal canal. It can no longer be doubted that the germ is not the miniature of the future being with all its organs, as Bonnet and Haller believed, but is merely "*potentially*," this being, with the specific vital force of which it is endued, and which it becomes "*actually*" by developement, and by the production of the organs essential to the active state of the "*actual*" being. For the germ itself is formed merely of amorphous matter, and a high magnifying power is not necessary to distinguish the first rudiments of the separate organs, which from their first appearance are distinct and pretty large, but simple; so that the later complicated state of a particular organ can be seen to arise by transformation from its simple rudiment. These remarks are now no longer mere opinions, but facts; and nothing is more distinct than the developement of glands from the intestinal tube, and of the intestinal tube itself from a portion of the germinal membrane.

very good

The creative organic force is not, like the mind, connected with one special organ.—If Ernst Stahl had been acquainted with the above facts, he would have been still more confirmed in his famous theory, that the *rational soul* itself is the primum movens of organisation; that it is the ultimate and sole cause of organic activity; that the soul constructs conformably to design, and preserves its body in accordance with the laws of its operation; and that by its organic action the cure of diseases is effected. Stahl's contemporaries and followers have partly misunderstood this great man, in believing that, according to his view, the soul, which forms mental conceptions, also conducts with consciousness, and designedly, the organisation of the body. The *soul* (anima) spoken of by Stahl is the organising power or principle which manifests itself in conformity with a rational law. But Stahl has gone too far in placing the manifestations of soul, combined with consciousness, on a level with the organising principle; the operations of which, though in accordance with design, obey a blind necessity. The organising principle, which according to an eternal law creates the different essential organs of the body, and animates them, is not itself seated in one particular organ; it continues in operation up to the time of birth in anencephalous monsters; it modifies the already existing nervous system, as well as all the other organs in the larvæ of insects, during their transformation, causing the disappearance of several of the ganglia of the nervous cord, and the union of others;

by its operation during the transformation of the tadpole to the frog, the spinal marrow is shortened in proportion as the tail becomes atrophied, and the nerves of the extremities are formed. This principle, thus acting conformably to design, but without consciousness, is also manifested in the phenomena of instinct. There is great beauty and truth in the saying of Cuvier, that animals acting from instinct are, as it were, possessed by an innate idea, by a dream. But that which excites this dream can be nothing else than the organising principle, the "final cause" of the being.

bad comparison ??

The existence of the organic principle in the germ, and its apparent independence of any special organ in the adult, as well as the fact that it is manifested in plants, in which both nervous system and consciousness are wanting, prove that this principle cannot be compared with mental consciousness, which is an after product of developement, and has its seat in one particular organ. Mind can generate no organic products, it can merely form conceptions; our ideas of the organised being are mere conscious conceptions of the mind. The formative or organising principle, on the contrary, is a creative power modifying matter, blindly and unconsciously, according to the laws of adaptation.

Origin of genera and species.—Organism, or the organised state, is the result of the union of the organic creative power and organic matter. Whether the two have ever been separate, whether the creative archetypes, the *eternal ideas* of Plato, as he taught in his "Timæus," have at some former period been infused into matter, and from that time forward are perpetuated in each animal and plant, is not an object of science, but of the fables and traditions which cannot be proved, and which distinctly indicate to us the limits of our mere consciousness. All that is known is, that each form of animal or plant is continued unchanged in its products, and that, in a roughly calculated number of many thousand species of animals and plants, there are no true transitions of one species to another, or of one genus to another; each family of plants and animals, each genus, and each species, is connected with certain physical conditions of its existence, with a certain temperature, and with determinate physico-geographical relations, for which it is, as it were, created. In this endless variety of creatures, in this regularity of the natural classes, families, genera, and species, is manifested one common creative principle, on which life generally throughout the world depends. But all these varieties of organism, all these animals, which are as it were so many modes in which the surrounding world may be enjoyed by means of sensation and reaction, are, from the moment of their creation, independent. The species perishes when the productive individuals are all destroyed; the genus is no longer capable of generating the species, nor the family of restoring the genus. In the course of the earth's history, species of animals have perished by the

revolutions of its surface, and have been buried in the ruins; these belong partly to extinct genera, partly to genera still existing.

The study of the successive strata of the earth, in which the remains of organic beings occur, seems to prove that the beings, which have thus left their remains on the earth, have not all existed at the same time, that the simplest creatures have first inhabited the earth; while the remains of the higher animals, and particularly those of man, are not met with except in the most superficial of the deposits which contain organic remains. But no fact justifies us in speculations concerning the original, or subsequent origin of living beings; no fact indicates the possibility of explaining all these varieties by transformation, for all creatures maintain unchanged the forms which they originally received.

Nature of the organic force.—The unity resulting from the combination of the organising force with organic matter could be better conceived, if it could be proved that the organising force and the phenomena of life are the result, manifestation, or property of a certain combination of elements. The difference of animate and inanimate organic matter would then consist, in that state of combination of the elements, which is necessary to life, having in the latter undergone some change. Reil has stated this bold theory in his famous treatise on the "vital energy,"* which some physiologists,—Rudolphi, for example,—regard as a masterpiece, on which the principles of physiology must be founded.

Reil refers the organic phenomena to original difference in the elementary combination and form of the organic bodies. Differences in the mode of combination of the elements and in form, are, according to his theory, the cause of all the variety in organised bodies, and in their endowments. But if these two principles be admitted, still the problem remains unsolved; it may still be asked, how the elementary combination acquired its form, and how the form acquired its elementary combination. That the form of the organic matter does not determine originally the mode of its action, is proved indisputably by the fact, that the matter from which all animal forms are produced is at first almost without form. The germ in all vertebrata, and probably also in the invertebrata, from what is known of a few species, and from what I have observed in the planaria, is a round disk of simple matter; here is no difference of form corresponding to the difference of the animals. On the other hand, the form of inorganic bodies is always determined by their elements, or by the combination of their elements. And this Reil himself admits; for he says: "Form of matter is itself a phenomenon, which depends on another phenomenon, namely, the elective affinity of the elements and their products." Hence it would follow, that if the elementary combination were alone the cause of the organic forces, this

* Reil's Archiv. für Physiologie, i. Bd.

elementary combination itself would be at the same time the formative principle. Now, since in organised bodies immediately after death the elementary combination does not appear to be different from that of bodies still living, Reil must admit the existence of other more subtile matters not recognisable by chemical analysis, which are present in the living body, but are wanting after death. Into the composition of the organic matter of the living body there must enter an unknown (according to Reil's theory, subtile material) principle, or the organic matter must maintain its properties by the operation of some unknown forces. Whether this principle is to be regarded as an imponderable matter, or as a force or energy, is just as uncertain as the same question is in reference to several important phenomena in physics; physiology in this case is not behind the other natural sciences, for the properties of this principle in the functions of the nerves are nearly as well known as those of light, caloric, and electricity, in physics.

At all events, the mobility of this principle is certain. Its motion is evident in innumerable vital phenomena. Parts frozen, stiff, and deprived of sensation and motion, are observed gradually to recover animation, which extends into them from the borders of the living parts. This passage of the vital principle from one part to another, is seen still more clearly on the removal of pressure from a nerve, after that state has been produced in which the limb is said to be "asleep." The fibrin effused in inflammation on the surface of an organ, is observed to become endowed with life and organisation. This organic principle exerts its influence even beyond the surface of an organ, as is shown by the changes produced in the animal matter contained in the vessels, for instance, in the lymph and chyle, which latter fluid during its progress through the lacteals acquires new properties; from the coats of the blood-vessels, again, the organic principle exerts an influence on the blood, maintaining its fluidity, for out of the vessels the blood coagulates under almost all circumstances, unless it has undergone some chemical change. Lastly, I may with Autenrieth adduce that property of animal tissues, by virtue of which vital energy is at one time withdrawn from them, and then again imparted to them, and is often quickly accumulated in one organ. I do not think that it is the influence of the vital energy which in an unincubated egg preserves the yolk and white from putrefaction, as Hunter remarks; but it is certain that an extravasated, enclosed, or morbidly collected fluid, even morbid animal matter, as pus, is preserved from putrefaction longer in the living body than out of it; which does not arise merely from the exclusion of air, since, when the vital powers are low, blood and pus rapidly undergo decomposition even in the body.* From all these facts the existence of a force which is often rapid in its action, and which moves through space, or of an imponderable

* Autenrieth, Physiologie, i.

matter, is evident; nevertheless we are by no means justified in regarding it as identical with the known imponderable matters, or general physical forces,—caloric, light, and electricity, a comparison which is refuted by any close examination. The researches on the so-called animal magnetism at first promised to throw some light on this enigmatical principle, or imponderable matter. It was thought that, by one person laying his hand upon, or passing it along the surface of another, and by other procedures, remarkable effects were produced, arising from the overflow of the animal magnetic fluid; some indeed have imagined that by certain operations they could produce accumulation of this hypothetic fluid. These tales, however, are a lamentable tissue of falsehood, deception, and credulity; and from them we have only learned how incapable most medical men are of instituting an experimental investigation, how little idea they have of a logical criticism, which in other natural sciences has become a universal method. There is no single fact relating to this doctrine which is free from doubt, except the certainty of endless deceptions; and in the practice of medicine there is also no fact which can be connected with these wonders, except the often repeated, but still unconfirmed accounts of the cure of paralysis by investing the limbs with the bodies of animals just killed, and the willingly credited fables of the restoral of youth to the old and diseased by their being in the proximity and exposed to the exhalation of healthy children, and vice versâ.

We have thus seen that organic bodies consist of matters which present a peculiar combination of their component elements, a combination of three, four, or more to form one compound, which is observed only in organic bodies, and in them only during life. Organised bodies moreover are constituted of organs,—that is, of essential members of one whole,—each member having a separate function, and each deriving its existence from the whole; and they not merely consist of these organs, but by virtue of an innate power they form them within themselves. Life, therefore, is not simply the result of the harmony and reciprocal action of these parts; but is first manifested in a principle or imponderable matter which is in action in the substance of the germ, enters into the composition of the matter of this germ, and imparts to organic combinations properties which cease at death.

Conditions necessary for the manifestation of life.—Vital stimuli.—The action of the vital or organic force is, however, not independent of certain conditions. The necessary elementary combination and the vital principle itself may be present, and yet not manifest themselves by the phenomena of life. This quiescent state of the vital principle, as it is seen in the impregnated germ of the egg before incubation, or in the seed of plants before germination, must not be confounded with the state of

Combustion. I should think is strongest analogy to life. — instead of heat being produced by the action. life — instead — destroying

death; it is also not life, but a specific state of "capability of living." Life itself, namely, the manifestation of the organic or vital force, begins under the influence of certain necessary conditions: these are warmth, atmospheric air, (in ova which are hatched in water, the air diffused through the water), and the supply of moist nutritive matters,—that is to say, of nutriment and water; and these conditions do not cease to be necessary for the continued manifestation of life.

The ovum of animals and plants remains in the state of germ only so long as it is maintained perfectly quiescent and beyond the influence of external agencies: it then remains capable of developement, and retains the creative force of the germ, but this force is in a quiescent state. The ova of animals will retain for a long period their capability of developement, while withdrawn from the influence of the atmosphere. Thus the productive power of the germ of the ova of many insects is preserved through the winter, and the ova of insects of transatlantic countries are hatched in the botanic gardens of Europe, an instance of which has fallen under my observation. In the same way the germinating power of the seeds of many phanerogamic plants is said to be preserved under water for twenty years, and in the ground beyond the influence of the atmospheric air for one hundred years.* Treviranus adduces the observations of Van Swieten that the seeds of the mimosa have germinated at the end of twenty years, and beans after two hundred years; and cites another observation, according to which an onion taken from the hand of an Egyptian mummy, perhaps two thousand years old, had been made to grow.† As soon, however, as it is subjected to the external influences above mentioned, the germ, when capable of developement, becomes developed, or it undergoes putrefaction; while the already developed organism, when the conditions necessary for its further growth fail, either falls into a state of apparent death, as in hybernation, or it dies. The quiescent vital force of the germ required no external stimuli for the maintenance of its passive existence; but these stimuli are very necessary for the developed and active life.

Action of the vital stimuli.—The external conditions which are necessary to life,—caloric, water, atmospheric air, and nutriment, at the same time that they maintain life, induce constant changes in the composition of the organised body; themselves combining with the body, while certain old components are again decomposed and cast off. These external agencies have been called *vital stimuli;* they must, however, be carefully distinguished from many other accidental stimuli which are not essential to life; and it must always be remembered, that these vital stimuli produce the phenomena of life by effecting

* Ann. d. Sc. Nat. t. v. 380.

† Treviranus, Erschein. ū Gesetz des Organ. Lebens, p. 47.

material changes, by producing an interchange of ponderable and imponderable matters. The essential elementary combination of the fluids, for example the blood, is by their agency constantly maintained, and the blood having suffered the necessary change by the action of the vital stimuli, in its turn stimulates all the organs of the body,—that is, produces in them organic changes of composition, essential to the manifestation of life, by the interchange of ponderable and imponderable matters, the old components of the organs being at the same time in part decomposed and cast off. In animals the nerves also effect important material changes in the organs; and their active force, probably an imponderable agent, is an important *internal vital stimulus.* The property of organised bodies of suffering constantly, by the action of the vital stimuli, certain material modifications necessary to the manifestation of life, has been termed *incitabilitas, excitability* (Reitzbarkeit). The stimuli are as it were the external force which sets in motion the wheels of the whole machine; and although the comparison of the animal body with a machine may not be very apt, yet the organic principle which in the organised body creates the mechanism necessary to life, is incapable of activity without this external impulse, and without the constant material changes effected by the aid of the external vital stimuli. Richerand has, therefore, not unaptly compared the manifestation of life with the phenomenon of combustion and flame. The appearance of fire endures only as long as the combinations and decompositions essential to combustion take place; the oxygen unites with the burning body, caloric is developed, and so long as oxygen and the combustible matter are supplied, the phenomena of fire continue. I am very far from making life dependent on combustion; I merely say, that, in both, certain essential combinations and decompositions are constantly going on, which in the one produce the phenomena of combustion and light, in + the other those of life; that the vital stimuli are for the organised body, what the oxygen of the atmosphere and the combustible matter are for the phenomena of combustion; in which case, however, the oxygen is not called the stimulus of the flame: and I further say, that the name stimulus, vital stimulus, gives an empty and indeed false notion, unless the material changes,—the constant new combinations and decomposition of ponderable and imponderable matters—induced by it be at the same time remembered. It is, however, necessary always to recollect, that in the material changes effected by the vital stimuli, although inorganic substances come into play in them, binary compounds are not generated for the organism, but only cast off as the result of the decomposition of the old matter; such a product is carbonic acid: while the oxygen, which in the process of respiration partly enters into combination with the blood, produces a certain change in this fluid, which in its turn must produce in the organs endowed with the

+ - The vital principle - produces the organs -- as the latter vary, so must the vital Principle.

vital principle, material changes very different from those that would be expected in a dead body.

These general essentials of life, the *vital stimuli*, or renovating (integrirende) stimuli, are common to plants and animals: for plants, *light* is also an indispensable vivifying stimulus; for animals, although the want of its influence renders the body scrofulous and rickety, it is not immediately necessary, as is proved by the life of many animals, particularly the entozoa, and its absence is only so far injurious as it modifies the other essential vital stimuli. As an essential for animal life must be reckoned not merely the assumption of new matter, but more especially of matter already organised; while plants take up as nutriment organised matters partly converted into binary compounds, and change these binary into ternary compounds. The necessity of new matter, caloric, water, and atmospheric air for the developement, subsistence, and growth of organised bodies, is quite indispensable.

Deep water sea weeds!

A great error has been committed in classing the *vivifying stimuli* with other stimuli, which do not essentially enter into the composition of organic bodies, and do not renovate their powers. A mechanical stimulus, which modifies the condition of a membrane endowed with sensibility,—for example, pressure,—excites, it is true, a vital phenomenon—sensation, but does not vivify, does not invigorate the organic forces; while, on the contrary, the essential vital stimuli really contribute to the formation of the organic matter. The *nutriment*, in the first place, is not merely a stimulus of the organic body; it is itself susceptible of life, it is a stimulus which vivifies, and can itself be vivified. Man, in the healthy state, can scarcely dispense with food for longer than a week without fatal consequences; the higher brutes do not live many weeks without it; reptiles, on the contrary, have been known to fast for months,—this has been chiefly observed in serpents and tortoises. *Water*, whether it enters as such into the composition of the organic matters, or contributes its elements to their composition, is also absolutely essential in its uncombined state to the manifestation of life, since the animal tissues, unless they are moist with water, are incapable of living. *Atmospheric air* is so essential for the manifestation of the vital phenomena, that in the higher animals life does not subsist a moment without respiration, without the changes in the blood effected by respiration, and without the influence of blood so changed upon the organs. The supply of nutriment, and the assumption of new matter from the blood into the organs, may be suspended for a considerable time, particularly in reptiles; but this other change, which the blood effects in the organs by virtue of its aeration in the lungs, can be suspended in reptiles but for a short time, in man only for a few seconds. *Caloric*, lastly, which is especially important at the time when the animal system is itself yet unable to generate any heat, but is indispensable for all organic beings, plants and animals, seems

also to enter into the composition of the organic system. For the organic processes require in every animal and plant a certain temperature; and it is also known, that in chemical processes among binary compounds, while a certain temperature is required, a determinate quantity of caloric becomes latent, or is absorbed for the formation of new compounds. Under the influence of the vital stimuli,—nutriment, water, air and caloric,—the organic being is developed spontaneously from the germ, while the organic matter present in it is constantly undergoing decomposition, and the phenomena of life are themselves the results of the constant union of new and the separation of old elements of the organised matter. Whether electricity also is necessary to the developement of life is at present quite uncertain.

There is, however, an evident *difference in the degree in which living beings are dependent on different vital stimuli.* M. Edwards has observed, that newly-born warm-blooded animals have most need of external warmth, and without it cannot live; while they can live under water, without breathing, much longer than adult animals. The time that they can remain in the water is longer in proportion as the temperature of the water rises from 32° to 68° Fahr.; remains the same when the water is between 68° and 86° Fahr.; and becomes shorter between 86° and 104° Fahr.* The adult animal has, according to the vital relations of its species and genus, a certain temperature, and consequently a certain geographical tract, assigned to it in which to live.

The duration of irritability without the application of the vital stimuli, is generally in the inverse ratio of the perfection of the organisation. The simplest animals can longest dispense with these stimuli. Mollusca and insects, as well as the scorpion, have been kept for months without food.† Serpents and tortoises also live for months without food, while man in the healthy state can scarcely survive a week. Several insects will live for days in mephitic gases; the larvæ of the œstrus, for example, according to the experiments of Van der Kolk, live for a long period in irrespirable gases. Molluscous animals have been kept during 24 hours under the air-pump. Reptiles live a very long time without respiring; in water deprived of its air some few hours, according to Spalanzani and Edwards, and in water still containing air, from 10 to 20 hours: frogs, the lungs of which I had extirpated, lived 30 hours. The numerous accounts, however, of toads, &c. having been found living in blocks of marble, and in trees, are to be regarded as instances of deception and credulity, although Herissaut and Edwards kept reptiles alive for some little time enclosed in gypsum. But Edwards is convinced that gypsum is permeable to atmospheric air; when the reptiles were

* Edwards, De l'influence des agens physiques sur la vie. Froriep's Notiz. 150, 151. See also Legallois, Exper. sur le principe de la vie.

† See my paper on the Scorpion, in Meckel's Archiv. 1828.

surrounded both by gypsum and mercury, they died as quickly as if under water.* The greater complication of the organisation increases the state of dependence of the organs on each other. Simple animals therefore live longer after injuries, than animals higher in the scale. Revival from the state of apparent death is much more easy in the lower animals. Spallanzani and Fontana saw wheel-animalcules, which had suffered desiccation, recover the appearance of life on being moistened with water. Ehrenberg, however, denies that this could occur. Steinbuch and Bauer have observed the same fact with regard to the vibriones of diseased wheat and of an agrostis; they revived when the grain was moistened, after an interval of years. After the most severe injuries, reptiles present signs of life for a long time; and the long persistance of irritability in the muscles and nerves of these animals is well known. The signs of life continue for a longer period in young animals also, probably on account of the greater simplicity of their structure. In the embryos of rabbits, I have seen the muscular irritability continue longer after death than in adult rabbits; and a fœtal rabbit removed from the uterus retained its life for fifteen minutes under the air-pump. On this point, Legallois has made some interesting experiments, the result of which is, that on killing rabbits by immersion in water, excision of the heart, or opening the thorax, on the first, fifth, tenth, and so on every fifth day until the thirtieth day after birth, it is found that the duration of sensibility is less every fifth day; so that, while on the first day it continued fifteen minutes, on the thirtieth day it endured only two and a half minutes. Legallois observed the same relation with regard to the persistance of the circulation after the spinal cord was destroyed, and the head cut off. All these facts are fully explained by the law, that the more developed the individual parts of a whole are, the more dependent they must be one upon the other.

Organised bodies are subject to death.—While life is continued, with an appearance of immortality, from one individual to another, the individuals themselves perish; but if *all* the individuals of a species are destroyed, the species itself, whether of animals or plants, becomes extinct, as the history of the earth proves. The *vital* or *organic force* flows, as it were, in a stream from the producing parts into those ever newly produced, while the old parts perish. This is well described by Autenrieth: "Those organised bodies only," he says, "which constantly strike fresh roots,—as the creeping plants, for example, by means of runners; or, as many trees, by means of descending branches,—do not die. In all these cases the new sprout forms, at one period, a part of the old individual, at the same time that it is a new and independent being. But even in these plants the old stem always perishes, and the *vital force*

* Edwards, in Meckel's Archiv. iii. p. 617.

continues active only in the new offset, which in its turn continues to extend itself on the one side, while it dies on the other. What here takes place connectedly,—namely, the decay on the one side, and the formation of a new living body on the other,—is effected in an interrupted manner in man and the more perfect animals. The young is separated from the parent as a new living body, before the old being perishes; and the original *individual* dies, while the *species* seems to be immortal."*

Cause of death.—Why organised bodies perish, and why the organic force is transferred from the producing parts of organic beings to the young living products, while the old producing parts perish, is one of the most difficult problems of general physiology. We cannot solve it, but can only describe the phenomena in their connection. It would not be sufficient to say that inorganic influences gradually destroy life; for in that case the vital force would begin to diminish from the very commencement of existence; and it is well known that at the time of virility the vital force is in such a state of perfection that it multiplies itself by the formation of germs. There must then be some other more occult cause, which induces the death of the individuals, while it ensures the propagation of the vital force from one individual to another, and in this way secures it from perishing. It might be asserted that the increasing fragility of organic bodies in old age arises from the increasing accumulation in them of certain products of the decomposition of the organic substance, the chemical affinity of which matters at last balances the vital or organic force; but in that case, also, the vital force must diminish from the very commencement of life; and there is besides no proof of such accumulation taking place. All that can be done, therefore, is to show the connection of these phenomena with developement. If the germ of an organic being is compared with its state in extreme age, it is seen that, at the latter period, the *whole*, on which, according to Kant, the existence of the *individual parts* depends, subsists almost solely by the reciprocal action of the individual parts and of their forces, like the working of a piece of machinery, which is maintained solely by the reciprocal action of the parts of the machine on each other; in the germ, on the contrary, the force, in which is seated the producing cause of all the parts of the future body, is still undivided. The organic principle in the germ is, as it were, in the state of the greatest concentration. The capability of developement is at its highest degree, developement itself at its lowest. When the operation of this principle has endured for a certain time, when the period of youth is passed, this state of simplicity, in which the whole force is undivided, no longer exists; there is then a state of complication, in which the force is divided among the different parts.

* Autenrieth, Physiol. i. 112.

But the more the single organic force of the body becomes divided, and the less of this force remains unapplied, so much the more does the organism seem to lose the property of becoming vivified by the influence of the general vital stimuli; and the less strong becomes, as it were, the affinity between the organised substance and the stimuli, which seem to nourish the flame of life. Therefore, when developement is complete, if the immortality of the vital force is to be secured, the formation of a germ is necessary. The germ, containing the vital principle in an undivided state, also possesses the greatest affinity for the vital stimuli, and this affinity again diminishes in proportion as the organism is developed. This has the appearance of explaining the phenomena, but is in reality merely a statement of their connection, and it is not even certain that the statement is correct.

Why organic matter perishes.—The cause of the constant destruction of the matter of organic bodies during life, and of the necessity for its being replaced by new organic matter, is the second point to be investigated. In plants this change of material is less remarkable, and is seen, to a great extent at least, only in the gradual death of the old leaves: in plants, as Tiedemann remarks, what is once formed, is for a long time subject to no change of material, but retains, for a certain period, its first composition. In animals, on the contrary, there is a constant renewal of the component matter. This difference between animals and plants, Tiedemann explains, by supposing that in animals there are certain functions, the performance of which induce changes in the material composition of the organs, as seems to be the case in the action of the nerves.*

M. Sniadecki's theory.—M. Sniadecki, who has endeavoured to solve this problem,† calls the substances which are capable of nourishing organised bodies, *matters susceptible of animation.* The susceptibility of animation with which these matters are endowed, is however quite general; they are capable of taking any form as long as they are not subjected to special influences, and for that reason are without special form. Organic matter then has, as M. Sniadecki expresses it, a general tendency to life and organisation. But as soon as any part of it comes within the influence of any individual being, the vital force of the individual gives a special direction to this general tendency; hence the individual and local conformation, and the different modes of life. Every special form of organisation is thus, according to M. Sniadecki, the result of two tendencies; one general, which resides in the matter itself, and by virtue of which certain substances strive towards life and organisation generally; and a second special tendency, which exists in the individual, and this latter determines the mode in which the life shall be manifested,

* Physiol. i. p. 376.

† Theorie der organischen Wesen, aus dem Polnischen. Nürnberg, 1821.

and the form in which the organisation shall be effected. This particle of vivifiable matter, therefore, which has been subjected wholly or in part to the influence of the vital principle of a certain individual, has acquired a proportional degree of vitality; but, as it has not ceased to be susceptible of life, it must, in virtue of this susceptibility, still tend towards further life, and to the assumption of all the other forms of organisation,—that which it already possesses being alone excepted. If this particle of matter is now compared with the organic matter, which is as yet quite unorganised, and which has an equal tendency to assume all forms, it is evident that it must possess less susceptibility of life than the latter. The diminution of its susceptibility of animation must be commensurate with the tendency which it had to take the particular form in which it exists, this tendency being already satisfied.

From this reasoning M. Sniadecki concludes, that the capacity of the matter in organised individuals for life, is in the inverse ratio of the vital force to which it has already been subjected; or, in other words, the matter which is taken into organised bodies loses just as much of its capacity for life as it gains of individual power; consequently, in the same proportion as it assumes a given form, it loses its faculty of assuming that form. As soon, then, as it is completely organised, and has undergone the whole vivifying power of the individual, it loses all susceptibility of organisation in reference to this individual. The vital force of the individual then loses all power over it; and this matter will, in the midst of the living body, be incapable of living and inert, and consequently only fit to be discharged from the body. In this way Sniadecki explains the constant change of organisable matters in organised bodies.

If this explanation is adopted, the general processes in organised bodies can certainly be further explained, as has been done by M. Sniadecki with admirable simplicity and clearness. Strong objections, however, may be urged against it. According to M. Sniadecki's doctrine, the only essential part of organised bodies is, not the organised matter, but the organic force. The force manifests itself as long as its organising action is continued; that is, as long as matter susceptible of organisation is present: the organised matter itself possesses no organic force, and is excreted from the body as being useless. But, according to this view, the excrementitious matters ought to bear the character of complete organisation, and should be susceptible of immediate organisation by other beings. This is not the case. The excrementitious matters of most general occurrence are the urine, and the carbonic acid which is exhaled in respiration. But these substances are not susceptible of organisation by other animals; they are the products of the decomposition of animal matters.

Author's views.—It is much more consonant with facts to suppose that

the matter assimilated by an organised body becomes endowed with the organising power at the moment that it is organised. The organising force itself is in many simple organic beings divisible, by division of the organised matter. We are thus led to the very opposite conclusion to that of M. Sniadecki. He maintains that the matter loses its capacity for life in proportion as it is endowed with life. We say, matter becomes vivified in proportion as it has experienced the vivifying force; it acquires the power of imparting life to other matter in proportion as it is itself vivified; and it exercises this power while acted on by certain *vital stimuli*, which, while they unite with the organised tissues, cause the separation and excretion of other substances. Certain *vital stimuli* entering the blood, as in the process of respiration, and then exerting their influence on the organised tissues, cause the affinity between certain elements of the organised matter and the blood to become greater than that between the different elements of the organised matter itself. The vivification of the organised matter by the vital stimuli, in a manner which is attended with excretion, renders it capable of receiving nutriment; but, in proportion as a portion of matter has life imparted to it, it acquires the faculty of giving life and organisation to other matters: it does not become excrementitious; on the contrary, it participates in the organising force of the original body.

The cause why organic substances are being constantly decomposed and cast off from the animal body, might at first sight be thought to lie in the following circumstance:—In the conversion of the food into matters proper for the nutrition of the body, some substances, from containing an excess of useless elements, may be necessarily ejected again. Thus plants, in forming ternary vegetable compounds from carbonic acid and water, give out the superfluous oxygen. In animals the only excrementitious matters of any consequence, which are quite useless in the organic system, are the carbonic acid and the urine. The excretions of animals, it is true, nearly equal in quantity the matter taken into the body; but in part they are purely useless excreta: many are destined for particular purposes, or are evacuated accidentally, as the mucus of the intestines, and perhaps also the bile. The fæces consist partly of substances taken as food; whereas the urine and carbonic acid are separated from organised tissues, and are perfectly useless to the system. The urine certainly varies in its composition according to the nature of the food, and therefore evidently contains also useless components of the yet unorganised food. But the composition of the urine remains unaltered in animals which live without food even for months, as many reptiles, serpents, and tortoises will do. The urine, therefore, it is certain, must be a means of carrying out of the system parts of the organised components which have become useless; and it is evident that the vital actions themselves are attended with decomposi-

tion of organic matter. Thus even the pupæ of insects at the period of their transformation, when they take no nourishment, afford excrementitious matter by means of the Malpighian vessels; and Wurzer, Brugnatelli, and M. Chevreul have shown us that these vessels secrete lithic acid. The embryo of the higher animals, also, forms a peculiar excretion by means of the Wolffian bodies, even before the kidneys have assumed their function.

It is remarkable, also, that urea and lithic acid are excreted by many invertebrate animals as well as by the vertebrate; thus insects, as we have said, secrete lithic acid by the Malpighian vessels, and M. Jacobson has discovered lithic acid in a special excretory organ in molluscous animals. We have not the most distant conception of the cause which renders the reciprocal action of the atmospheric air with the living body so necessary to life; but the hypothesis that respiration supplies the elements still required for the formation of animal matter, or removes the elements superfluous to this compound, is refuted by the facts that most animals take the animal matter ready formed, and that reptiles continue to respire, to consume the oxygen of the air, and to exhale carbonic acid, when they take no food for months.

The excretions which are being constantly formed by the vital process even without food being taken, namely, carbonic acid and urea, (and lithic acid,) are incapable of nourishing other animals. Carbonic acid is a binary compound formed by the decomposition of animal matter: urea is very analogous to a binary compound, and is perhaps really one; at all events, Woehler has shown that it is produced from cyanite of ammonia with extreme ease. As these excretions are constant, even when the supply of nutriment is stopped, it necessarily follows that a constant decomposition of the substance of the body is essentially connected with life. It cannot indeed be otherwise, if it be true, as it has already been proved to be, that the vital force is manifested in an animal only while certain vital stimuli produce in the living tissues constant material changes, of which the phenomena of life are merely the external signs, just as flame is the appearance resulting from the material changes effected in combustion. The impulse to these material changes is given by respiration; the blood, undergoing a constant change by respiratory process, again effects constant material changes in the organs to which it is distributed: from the former components of the tissues are formed the general products of decomposition,—carbonic acid, and the substances so rich in nitrogen which are found in the urine, urea and lithic acid;—and this decomposition of the materials of the body, which constantly attends the vital process, in its turn renders necessary the supply of new nutritive matters, which are subjected to the organising force. An organised part presents vital phenomena, and organises new matter, only while excited by the constant exertion of organic affinity

between the blood and the components of the tissues; by the exertion of which affinity certain components of the organs are decomposed, their place being again supplied by new nutritive matter acted on by the organic force.

Sources of new organised matter.—The nutriment of animals consists of organic matters, animal and vegetable; the nutriment of plants consists partly of vegetable and animal matters not wholly decomposed, and partly of binary compounds, namely, carbonic acid and water. It has been imagined that plants can nourish themselves from carbonic acid and water alone; the experiments of Hassenfratz, M. de Saussure, Giobert, and Link, have proved however that plants under these circumstances, if they grow at all, do so very imperfectly, and seldom flower and bear fruit.* It appears, therefore, that it is only when they are at the same time nourished by organic compounds in solution, which have not wholly undergone decomposition, that plants generate organic matter from binary compounds.

The power of generating organic from mineral compounds cannot, however, be entirely denied to plants; for, were it not for this power, the vegetable and animal kingdoms would soon perish. The unceasing destruction of organic bodies presupposes the formation by plants of new organic matter from binary compounds and elementary substances.

The organic force also is increased during the organisation of new matter.—Now, by the growth and propagation of organised bodies, the organic force seems to be multiplied; for from one being many others are produced, and from these in their turn many more; while, on the other hand, with the death of organised bodies the organic force also seems to perish. But the organic force is not merely transmitted, as it were, from one individual to another,—on the contrary, a plant, after producing yearly the germs of very many productive individuals, may still remain capable of the same production,—the source of the increase of the organic or vital force seems therefore also to lie in the organisation of new matter; and, this being admitted, it must be allowed that plants, while they form new organic matter from inorganic substances under the influence of light and caloric, are also endowed with the power of increasing the organic force from unknown external sources, while animals also in their turn would generate the organic force from their nutriment under the influence of the vital stimuli, and distribute it to the germs during propagation. Whether during life the organic force, as well as the organic matter, is constantly suffering destruction, is quite unknown. Thus much however seems certain, that, at the death of organic bodies, the vital force is resolved into its general natural causes, from which it appears to be generated anew by plants. If this increase of the vital principle

* Tiedemann's Physiolog. i. 218. Translation, p. 83.

in existing organised bodies from unknown sources in the external world be not admitted, it must be supposed that the apparently endless multiplication of the vital force in the process of growth and in propagation is merely an evolution of germs encased one within another, or it must be admitted that the division of the organic force which takes place in propagation does not weaken its intensity; a supposition which appears absurd. But the fact would still remain, that, by the death of organised bodies, organic force is constantly becoming inert, or resolved into its general physical causes.

3. *Of the Organism and Life of Animals.*

Differences of plants and animals. — Developement, growth, excitability, propagation, and decay, are the general phenomena and properties of all organised bodies, and are the results of organisation; but there are other properties peculiar to animals, which may therefore be termed *animal* in contradistinction to the general *organic* properties. Sensation and voluntary motion are the more remarkable *animal* properties.

Motions of plants. — Plants, it is true, are not wholly without motion, for their organisation is attended with internal motions, namely, the circulation of the sap; moreover, they turn spontaneously towards the light, their roots extend in the direction of the most nutritious soil: some plants climb along the surface of bodies which offer them means of attachment, and their stamens incline towards the pistil at the time of impregnation; many plants indeed, particularly those of the genus mimosa, possess in their leafstalks a power of motion which can be excited by various irritants, whether mechanical, galvanic, or chemical—such as alcohol, mineral acids, æther, and ammonia,—as well as by change of temperature or light; thus affording another instance of the general law, that the specific excitable properties of organic bodies do not vary in the mode of their manifestation according to the nature of the stimulus which excites them, but are manifested each in its peculiar manner on the application of the most different stimuli.* Lastly, in the hedysarum gyrans there is, besides the general influence of light on the motion of the larger middle leaflet, an incessant rising and falling of the two lateral leaflets, independent of external stimuli; and some of the lower vegetables—the oscillatoria, for example,—present a constant vibratory motion. The twining of certain plants is supposed by Palm† to be dependent on their mode of growth causing the extremity of the branches to describe circles, thus enabling them to lay hold on near objects: but, however this may be, the fact that the cuscuta twines only around living plants, seems to show that, in it, this motion is in some measure

* Treviranus, Biologie, v. 201. 229.

† Palm uber das Winden der Pflanzen, p. 48.

dependent on organic attraction; and the motions of stamens and leafstalks have too much resemblance to the irritability of muscles, not to be compared with it. Dutrochet* has discovered, that in the mimosa the irritability resides in the cortical part of a swelling situated at the articulation of the leafstalks. When this swelling, which exists in those mimosæ only which possess this irritability, was removed, no motion could be excited; when the upper half only was cut away, the leaf was elevated, but not depressed again. Hence Dutrochet infers that the elevation and depression of the leaf and leaflets arise from incurvation of the opposite sides of the swelling; elevation being produced by the lower part of the swelling becoming convex, depression by a similar incurvation of the upper part. Slices taken from the cortical part of either the upper or under half of the swelling, when placed in water, are seen to become curved. Other physiologists, Lindsay, Ritter, and Mayo, have observed a change of colour at the time of the movement, so that the phenomena might be attributed to an afflux of sap to either side of the swelling.†

Motions of animals.—There are then, in plants, organs which, by their motions, resemble either the muscles or the erectile parts of animals; but there is this difference, that the motions of animals are not merely the result of the action of a stimulus on irritable parts, but are produced by the internal operation of parts not endowed with motion, namely, the nerves, on those which have motion. Dutrochet, it is true, has observed that, when he directed the focus of a burning-glass on a single leaf of the mimosa, the impression was propagated gradually to the other leaves; and he considers the false tracheæ, or ducts, to be the organs which transmit this influence. But, as Treviranus justly remarks, this is merely an hypothesis; for other observers have perceived only the local effect of concentrated light, and, besides, the shock produced by the local motion may be sufficient to excite motions throughout the whole plant.

Another remarkable character of a part of the motions of animals is, that they are excited, not merely in accordance with the harmonious action of the whole organism, but by the voluntary operation of a single organ, namely, the organ of the mental faculties. These motions are voluntary. Irritability again must not be confounded with sensibility. Plants are irritable, but not sensible; the muscles also when separated from the animal body are still irritable, but they are not sensible. Plants cannot be affirmed to possess sensibility, unless they manifest consciousness. Manifestations of sensation and voluntary motion are the sole characteristic mark of the simplest animals. Compound animals have often a

* Recherches Anat. et Physiol. sur la structure intime des animaux et des vegetaux.

† Tiedemann's Physiologie, i. 623. G. R. Treviranus, Erscheinungen und Gesetze des organ. Lebens.

ramified and vegetable form, and are fixed by a stem to the ground; the individual faculties of the single polypes,—the voluntary motion of each polype,—indicate however, that they have an animal organisation *(organisatio animalis multiplicata)*, and by no means that of vegetables. The movements of infusoria are free and voluntary. If, therefore, it is still a matter of doubt whether certain simple organised beings, such as the sponges and several so called alcyonia, are animal or vegetable, the absence of all voluntary motion in these bodies, whether of the whole or of individual parts of it, must determine the question, and they must more properly be numbered among the vegetable marine structures. It may certainly be said that the embryo of sponges, as Dr. Grant* has shown, like the embryo of polypes and corals, moves by means of cilia; but the distinctive marks between the embryo of sponges and marine infusoria are by no means certain, and similar motions have been many times observed in the embryo of true vegetables,—of the algæ, for example.† The movements of the ova of zoophytes by means of cilia, are not to be regarded as voluntary; the vibrations of cilia on the branchiæ of some of the lower animals are a similar phenomenon. It would appear from the researches of Nitzsch‡, that some vegetable and animal products of infusions are very closely allied to each other. Thus the bacillaria pectinalis, and other species of this genus, would seem to have completely the characters of plants; while other species again have the characters of animals. Ehrenberg, however, seems not to admit the existence of such a relation between the two kingdoms; he remarks also that the active movements of algæ should not be regarded as proofs of animal life, for he has never seen the moving sporules of algæ take the slightest solid nutriment; and thus, according to M. Ehrenberg, the algæ scattering their ova or sporules differ from monads, as a tree differs from a bird. §

* Edinb. Philos. Journ. vol. xiii. p. 382.

† This has been observed by Trentepoil with respect to the conferva dilatata, β, Roth, or ectosperma clavata, Vauch., and by G. R. Treviranus with respect to the conferva limosa, Dillw. See Treviranus, Biologie, t. iv. p. 634. Recently Unger has repeated these observations, in watching all the transformations in the conferva dilatata; and it appears, as Treviranus also maintains in opposition to Vaucher's supposition, that the presence of infusoria had given rise to error, that these originally moving gemmules are again converted into algæ from which they were produced. See Unger in Nova Act. Acad. Nat. Cur. t. xiii. p. 2, p. 789, and Treviranus in the Biologie, t. iv. and in Erschein. und Gesetz. des organ. Lebens, p. 51 and 183. This motion of the embryo of vegetables is also instanced in the Zoocarpées of Bory St. Vincent, which, themselves jointed threads, emit germinal granules, which move about like infusoria, and then again assume the vegetable form; these he places together with the whole tribe of arthrodiées, in a class intermediate between the animal and vegetable kingdom.

‡ Beiträge zur infusorienkunde. Halle, 1817.

§ Poggendorf's Annal. 1832. 1.

Professor R. Wagner is led by his own observations to adopt the same opinion; he remarks, that the motions of these germinal granules cannot be regarded as an animal act, although it appears more wonderful than the regular motions of some of the lower vegetables, namely, the oscillatoria.

Animals have a nervous system.—The sensations and other incitements to voluntary motion,—the true animal functions, in fact,—are dependent on the nervous system. The organs of animals manifest as great a dependence on the nerves as the plants on light. Nerves were known to exist in all vertebrate animals, but they had been discovered in a part only of the invertebrata; and the opinion was very general, that the lower animals have no nerves, all the functions of sensation, motion, and digestion being performed by the same particles of their simple substance. The great divisibility of the lower animals seemed indeed to justify, in some measure, this conclusion. The nerves were not known to exist in the infusoria, polypifera, acalepha, and most of the entozoa. But Otto had already described the nervous system of the strongylus gigas, a worm of the kidney. In the round worm, the nervous cord between the two vascular trunks is very evident. Mehlis has described the nervous system of the distoma hepaticum, Nordmann that of the pentastoma and diplozoa. There is no doubt but it exists in all the intestinal worms. Tiedemann discovered the nervous system of the echinodermata; at least, that of the asterias. Lastly, Ehrenberg* has shewn the existence of a complex structure in the lowest animals, the infusoria. In the simplest infusory animalcules Ehrenberg has discovered a mouth and compound stomach; in others, mouth, intestine, and arms. In the more perfect rototoria, and in some infusoria, Ehrenberg has even described, and represented very distinctly, a kind of teeth in the mouth, male and female organs of generation, muscles, ligaments, a trace of vessels and nerves, and eye-points. These points, which Ehrenberg believes to be real eyes, are of especial importance for the question of the existence of a nervous system in the simplest animals. On the head of planariæ, in which no nervous system has hitherto been discovered, exactly the same eye-dots have been seen as exist in many annelides, which are known to have a nervous system; from which circumstance, and from the fact that the eye-dots of some nereides are really formed of an enlargement of the optic nerve, with a cup-like covering of black pigment, it is very probable that the planariæ also, and indeed all the lower animals which have such eye-dots, really possess optic nerves, and consequently a nervous system.† It becomes indeed more and more probable that all animals,

* Organisation der Infusionsthierchen. Berlin, 1830.

† If Gruithuisen believes that every dark spot of the skin has a certain relation to the function of vision, his reasoning is quite inexact; for the first condition for vision

without distinction, have a nervous system. The difficulty of distinguishing the nerves of the asterias, and of several mollusca, teaches us that we must not attribute too much importance to the fact that even in larger animals, such as the actinia and medusa, there are no distinct traces of this system. [Ehrenberg † has recently discovered a nervous system in the medusæ, with red points, which he believes to be eyes.]

Digestive apparatus.—Animals are distinguished from plants, however, not merely by sensation and voluntary motion. These attributes necessarily modify the other functions which animals possess in common with plants. This is very beautifully set forth by Cuvier. Vegetables, fixed to the surface on which they grow, absorb immediately, by their roots, the nutritive particles of the fluids which permeate them; animals, on the contrary, which generally are not fixed to one spot, but either wholly change their situation, or at least, as polypes of a solid stem, seize their food, must have the means of carrying about with them the store of fluids necessary for their nutrition. By far the greater number have an internal cavity, into which they introduce the matters intended for their nourishment, and in the parietes of which arise the absorbent vessels, which, as Boerhaave aptly remarked, are true internal roots.‡ In some animals there is no anus, in others the existence of an intestine is doubtful. Nevertheless Mehlis states, in opposition to the common belief, that in the tænia there is a vessel-like intestine, commencing at the narrow oral orifice and soon becoming bifurcated. A well-known narrow bifurcated canal in the echinorhynchus is supposed to be the intestine. There is another cause than that above mentioned, for the necessity of a special cavity for the first process of assimilation in animals; the food of animals requires to be dissolved. The nutriment of plants is already in solution, and consists partly of water holding carbonic acid in solution, and partly of the dissolved organic matters of the soil, *humus.* The food of animals, consisting of compounds already organised, requires to be prepared, comminuted, and dissolved; hence digestion is a preparatory assimilation of the food, peculiar to animals.

The circulation in plants is much more simple than in animals, and is in no case provided with a special organ for the distribution of the

is, that the optic nerve shall have a special sensibility for light, and not be a mere nerve of sensation. Those lower animals which, without having eyes, are sensible of the influence of light, can be so only by reason of the warmth accompanying the light. Hence the annelides,—for example, some nereides,—without having a transparent optic apparatus for distinguishing different objects, nevertheless have nerves for the mere general perception of light and darkness; and the mere existence of optic nerves for the general perception of light in an animal which, from the absence of optic apparatus, can distinguish no definite object, is a strong proof that the perception of light is always connected with special nerves. See my Observations on the structure of the eye of the Nereides.—Annal. des Sciences Nat. t. xxii. p. 19.

† Müller's Archiv. 1834, p. 571.

‡ Cuvier, Anatomie Comparée, t. i.

fluid, namely, a heart. In some simple plants there is a rotatory motion of the sap in the interior of internodia and in cells. Corti discovered this motion in the chara, and his observation has been confirmed by Fontana, by G. R. and L. C. Treviranus, Amici, C. H. Schultz, Agardh, and Raspail; Meyen has discovered a similar motion in the cells of the vallisneria spiralis, and in the hairs of the radicle fibres of hydrocharis morsus ranæ. In the higher vascular plants Professor Schultz* has discovered a continuous motion of the sap, which according to Schultz, is a true circulation, ascending in one vessel, and descending in the other; the two streams, however, communicating by cross branches between the different vessels. In fine sections of the leafstalk of many plants it may also be distinctly observed that the course of the sap is different in different vessels; and this I have seen very distinctly even in fine sections of the leafstalk of fig-leaves. Whether the section, whether the division of the vessels, has not some share in determining the direction of the currents, can be ascertained only by observing the different currents in uninjured leaves. In leaves of the chelidonium which were still in connection with the living stem, I have certainly seen currents in opposite directions. The circumstance observed by Dutrochet, that an ascending and descending rotatory motion is produced in a perpendicular thin glass vessel filled with water, when it is heated differently at different parts, cannot be applied to explain the motion of the sap in plants; for in that case the sole cause of the rotatory motion is the ascent of the heated and expanded molecules of water. It appears, therefore, that the motion of the sap in plants is effected, in some manner at present not understood, by attraction and repulsion, exerted in the leaves on the one hand, and in the roots on the other. It is certain, however, that light exerts an attraction upon the sap, since it evidently determines the growth of the whole plant.

The circulation in animals, on the contrary, derives its impelling force, not from external influences, but from the contraction of a central organ, the heart. It is still uncertain whether a perfect circulation is an absolute predicate of animals; at all events, in many simple animals neither heart nor vessels have at present been discovered.

The respiration of animals and plants affords a very important distinctive character. In plants, and in the most simple animals, respiration is performed by the entire surface; but in the more perfect animals the surface is not sufficient for the necessary aeration of the fluids, and an organ is required, which in a small space shall afford an immense superficies for contact with the atmosphere. But the products of respiration in the vegetable and the animal kingdom are also different. In plants the

* Ueber den Kreislauf des Saftes im Schöllkraut. Berlin, 1822.—Die Natur der lebendigen Pflanze. Berlin, 1823.—Annal. des Sc. Nat. t. xxii. p. 75, 79.

assimilation of nutriment consists partly in the conversion of binary compounds, carbonic acid and water, into ternary compounds of the elements of these substances—into vegetable matter, in fact. In this process an excess of oxygen remains, which is then exhaled by means of the leaves. The leaves also absorb carbonic acid from the atmosphere, as has been proved by the researches of Priestley, Scheele, Ingenhouss, Spallanzani, Sennebier, Humboldt, and De Saussure. By the action of the leaves, the carbonic acid contained in the atmosphere is decomposed; the carbon and a part of the oxygen combine with the plant, while the greatest part of the oxygen is restored to the air. During the night, and in the shade, as well as in an unhealthy or fading condition, plants absorb a part of the oxygen of the atmosphere and exhale carbonic acid; but the quantity of carbonic acid thus exhaled is less than that which they ordinarily absorb during the day.* Respiration, then, in plants appears merely to serve for the correction of the assimilating process. The respiration of plants also removes from the atmosphere a part of the carbonic acid formed by animals, and yields to it an abundance of oxygen. Animals are nourished by organic matter only, not by inorganic matter; and besides carbon, oxygen, and hydrogen, nitrogen also, which in many plants is quite wanting and in others exists in very small quantity, enters into the composition of animal matter. From the circumstance that a large quantity of animal matter is constantly undergoing putrefaction, and is thus converted into binary compounds, while animals are quite incapable of generating new organic matter from simple elementary bodies or binary compounds, it is evident that plants, which have the latter power, are absolutely necessary to animals, just as animals on the other hand are indispensable for the existence of plants; for animals exhale that which plants inhale, namely, carbonic acid, and inhale that which is exhaled by plants, namely, oxygen. Hence, without the existence of the vegetable world, the atmosphere would become irrespirable for animals; while, by the reciprocal action of plants and animals, the composition of the atmosphere is preserved nearly absolutely unchanged.

Propagation by shoots and by division in plants.—Plants, having only one mode of manifesting life, namely, by *vegetation*, do not require manifold organs in addition to their roots, stem, and leaves; and, with the exception of the organs of fructification, present merely a repetition of perfectly similar parts, in all of which the simple relation of branches to leaves is the same; and even the sexual organs are evidently allied to the leaves, and in some cases are transformed into them. Moreover, a consequence of plants thus presenting before fructification merely a repetition of similar parts united by one stem is, that each of these parts

* Tiedemann's Physiology, Translation, p. 118. Gilby, Edinb. Phil. Journ. 1821, 7.

phenomena comprehends the processes which lead to the formation of new germs in an individual, and to the separation and developement of these germs; and consequently have for their object the preservation of the species, while the individuals perish.

The above mode of classification has its advantages, but may give rise to misconceptions. The force which determines the developement of the germ is identical with that which is the source of the constant preservation and renovation of the individual. The primary forces of the animal body would, therefore, appear to be the vegetative, the motor, and the sensitive forces; but it is again a question whether even this is not an artificial division.

It can be conceived that the essential principle of vegetable life,—the vegetative force,—may be combined in animals with other forces, namely, with the sensitive and motor, or with the nervous power, if the contractile power of the muscles is regarded as derived from the nerves, and not inherent in themselves. It may be imagined that these forces are united in the germ, and that, from the period of developement, they manifest themselves in the different systems of organs, which react on each other; so that the vegetative, directed by the nervous force, reproduces and constantly preserves the organs of nervous life as well as other parts, while the nerves again give sensibility to the parts organised by the vegetative force. If, however, this theory be reconsidered, it will be seen to involve contradictions.

It is much more probable that these apparently distinct forces are merely different modes of action of one and the same 'vis essentialis' resident in the animal, which modes of action are determined by the different composition of the organs. There is indeed an absurdity in the very idea that the nutritive force forms the nerves, and that the action of these nerves, when formed, results from a force distinct from that which formed them. The vital force creates in animals all the essential parts, and generates in them that combination of elements, the result of which in the nerves is the power of motion and sensation, or the power of conveying impressions to a central part, and reflex actions from it. The organs endowed with the power of assimilating matters which are destined for the use of the indivisible whole, the organs of motion, and the organs by means of which a central organ receives impressions from all the other organs and transmits its reflex actions, are only the different products of this first and sole principle of animal existence,—the primum movens, which produces and reproduces all parts of the body. The first set are the organs subservient to the renovation of the body, the second the muscles, the third the nerves. Then there are also parts which receive from the creative organic force merely the physical properties of hardness, elasticity, toughness, &c.—for example, the bones, cartilages, ligaments, and tendons.

The glands, for example, by nutrition and reproduction, acquire the property of attracting certain parts of the blood, combining them anew, and separating them from that fluid. By the same process of nutrition and renovation, the muscles acquire the property of contracting on the application of certain stimuli,—a property which is the result of nutrition, not a special force or principle distinct from the organic creative force. In the same manner the nerves receive the power of manifesting their vital phenomena, which again are merely the results of nutrition. Omitting from consideration those parts which receive from the nutritive force merely physical properties, the endowments of the other principal systems of the animal body may be indicated as follows:

1. *Organs which change the chemical composition of the fluids* for the purposes of the general system; such are the secreting organs, the blood-vessels and lymphatics, and the lungs. The peculiar function performed by these organs is not nutrition, for this is performed in all the organs of the body, but the change of the organic combination of the elements in fluids which are in contact with them, by exerting an organic affinity.

2. *Muscular organs*, which contract when acted upon by certain influences, their fibres becoming flexed in a zigzag form towards the spot where a change of their substance is produced, and thus shortened. Haller has named the property possessed by muscles of contracting under the influence of mechanical, chemical, and electric stimuli, *irritability;* and the *irritability* of Haller can be ascribed to no other than muscular parts, while other structures are characterised by the phenomena of a different kind of excitability. By some writers this term of irritability has been greatly misapplied; thus, they have spoken of an irritability in the nerves, as if at one time their irritability, at another their sensibility, could undergo a change. In the living body the action of the muscles is always determined by their nerves, and every cause which changes the composition of the nerves, although but slightly, produces a discharge, as it were, of the nervous force, and, as the result of this, a contraction of the muscles. Hence the study of muscular motions, and of spasmodic and paralytic affections generally, leads to the investigation of the laws which regulate the action of the nerves. Motion accompanies all changes of composition; it takes place in the processes of formation, nutrition, and secretion, and an organic affinity exerted between the blood and the tissues produces the motions which accompany *turgescence or erection:* muscles are not the only parts capable of motion, but they are the only organs which move by contraction and zigzag flexure of fibres; and all parts which are able to contract in this manner, although not essentially muscles, derive this power from muscular substance, particularly muscular fibres, intermixed with their tissue; such parts are the efferent ducts of glands, which are distinctly contractile.

has the power of becoming in its turn an independent living body when separated from the rest of the plant; for, besides the generation by seed, there is here a generation by shoots. The seed also is an independent part; the only essential point in which it differs from a shoot being, that in the seed the vegetative power is great, while vegetative action is very imperfect, or even does not exist.

In animals, on the contrary, the reciprocal action of circulation, respiration, and the nervous system, is actually necessary to life. The respiratory movements are dependent on nervous influence: but the nerves do not exert this influence unless supplied with blood which has been aerated in the lungs; and the blood again is not sent to the different organs, and therefore not to the nerves, without the contractions of the heart are performed; while the heart in its turn is dependent on the influence of arterial blood and of the nerves. The brain, heart, and lungs are therefore, as it were, the main wheels of the animal machine; which wheels react one on the other, and are set in motion, as it were, by the change of material which takes place in respiration. The growth of animals also is not effected by an external protrusion of new parts, but generally by enlargement of the whole animal—by increase in size of each original part internal as well as external. The compound polypiferous animals afford the only example in the animal kingdom of the mode of growth by new shoots. Most animals, and especially the more perfect, do not constitute an aggregate of similar parts united by one trunk; on the contrary, they contain parts of very different vital properties; and this circumstance renders propagation by division in them impossible, unless, as in the case of polypes and some annelides,—as the nereides and naides,—each of the separated portions still contains the essential parts of the whole.

The object of the entire of the foregoing comparison has been merely to show how the possession of new properties by animals modifies in them even those functions which are common to them and plants.

Classification of the functions of animals.—The comparison of animals with plants suggested to the earlier physiologists their mode of arranging the functions of animals.

The functions which plants and animals appear to possess in common, have been called *organic or vital;* they have for their end the production and maintenance of all the separate parts in the self-existing whole. They are the manifestations of organic affinity in the operations of the organic or vital force. The functions which especially distinguish animal beings, namely, sensation, motion, thought, &c. appear to be the end of animal existence; these functions it is which would characterize the animal, although it existed only a moment. The ancients named them *animal*, in contradistinction to the former, organic functions. A third series of

3. *The nerves* are in part motor, in part sensitive. The motor nerves are those which, under the influence of changes in their condition so slight as to elude the perception of the observer, excite motions in the muscles: the sensitive nerves are those which have the faculty of communicating every change which they suffer to the brain, the central organ, from which again certain influences are transmitted to all the other organs of the body. Many nerves, arising from the brain and spinal marrow, are, while in connection with these organs, voluntary excitors of motion in the muscles; while, under the influence of a change in their condition they may become excitors of involuntary muscular contractions, whether the connection between them and the brain and spinal cord is still maintained, or not. Those parts, on the contrary, which are endowed with motion, and are dependent on the sympathetic nerve, are withdrawn from the power of the will, and are only, in a certain degree, dependent on the brain and spinal marrow, through the medium of the connection of the sympathetic nerve with cerebral and spinal nerves. It is in the nerves that the mobility of the organic forces, without motion of the ponderable masses, is most manifest; their operation is necessary for the exercise of all the functions of the body, since all parts of the system, through the medium of changes produced in the nerves, react on the brain and spinal marrow, and receive from these organs certain influences necessary for their peculiar actions.

These systems of organs are interwoven in different manners one with another. The sensibility of any part is solely owing to the nerves which enter into its composition: the organs which serve to produce chemical changes in the fluids, if contractile, are so only by virtue of the muscular fibres which they contain; and when there is a secretion of fluids in a part endowed with other peculiar vital properties, there is always a peculiar tissue for this purpose; such, for example, is the case in the organs of sense, in which fluids are secreted by special tissues.

Organic attraction.—The reciprocal action of these systems of organs, and their nutrition from the blood, cannot take place without the manifestation of affinity in the ponderable and imponderable matters, together with organic attraction. A knowledge of the laws of this attraction would be of the greatest importance; but the facts relating to it which we are acquainted with, although remarkable, are very few in number; such are the attraction of the blood into parts which are capable of erection and which are at the time in a state of excitement, and that remarkable mode of union of germs by which a part of the double monsters are to be explained. Such a union of the germs could not have taken place without an attraction having been exerted between similar parts; for in almost all cases the monsters are united by their corresponding parts, face with face, snout with snout either by the anterior or lateral surface, occiput with occiput either by the middle or side,

neck with neck, breast with breast, or merely belly with belly, or side with side, or merely buttock with buttock; the uniting parts of the two embryos, in these cases, always becoming single, while the cavities of the two are double. A single actual observation of this organic attraction between minute parts would be of the greatest importance. But all my endeavours to obtain this desideratum by experiment have been fruitless: I placed the nerve of a frog exposed and dissected out under the microscope, and watched the end of the nerve while surrounded by blood-globules; again I placed some semen of the frog with portions of the unimpregnated ovum under the microscope; but in neither case could I perceive anything like organic attraction.

Animal excitability.—The laws of the excitability of organic beings generally, have been investigated in the former section; the relations which the vital stimuli bear to the manifestations of life have been there determined. The laws of the excitability of animals will be here more particularly set forth, although in the present state of science it is scarcely possible to throw any light upon this difficult problem, a knowledge of which however is so desirable, since it is here that practical medicine has much to expect from physiology.

Whether the vital principle or organic force is the result of the combination of ponderable and imponderable matters, or itself determines and maintains the peculiar composition of organic matter, it is an observed fact, that under certain circumstances this force becomes strengthened in particular organs, of which in this case the action becomes greater and more continued, as is observed in the genital organs during pregnancy and the sexual ardour. Thus also the organic force is observed to become less in the antlers of the stag just before they fall off, and to be again increased when they are reproduced in an organised state. An accumulation of organic force in a part is accompanied by an increased afflux of blood, and a more abundant conversion of blood into organised matter. Tiedemann remarks, that an organ in an excited state undergoes more rapid changes in its material composition, and therefore attracts more quickly and in larger quantity the blood, which alone is able to render an organ capable of increased vital action.* When, on the other hand, any organised part has suffered a lesion from change in its material composition, in that case also if the destruction of organised texture has not been too great, increased action ensues for the purpose of restoring the healthy state. Organised beings have the power of preserving in all parts the composition necessary for the life of the whole. When the composition is disturbed, the curative effect of this power is manifested. This is a necessary consequence of the law, that in organic bodies there is a constant striving to counteract chemical affinities. Hence the increased flow of blood to an injured part arises

* Tiedemann's Physiologie, i. p. 326.

from the organic action in it being increased. The reciprocal action of the increased organic process, and of the commencing tendency to decomposition in the part, on each other, is seen in inflammation. Inflammation is not essentially a state of increased action, but is compounded of the phenomena of the local injury, a tendency to decomposition in the part and increased vital action striving to balance the destructive tendency. When the degree of change of composition in the animal tissues is greater, reaction does not ensue, and inflammation is not produced; such is the case in death by narcotic poisons. When inflammation does occur, the change produced by the injury may soon become so great that the organic reaction is not able to counterbalance it, and local death ensues.

Exhaustion.—These and many other cases, even the fatigue and exhaustion which follow great exertions, show that the organic force is consumed as it were by the exercise of the functions. This circumstance is evident even after death; for if we take two similar portions of muscle of an animal just killed, and excite in the one slight contractions with a knife, while the other is left unirritated, the first portion will lose its irritability sooner than the other, and the difference will be proportionate to the number of contractions which have been excited in it.* In the same way every impression of light deadens the power of vision in some degree, and an equal stimulus immediately afterwards does not produce an equal reaction; the eye requires rest.

This might be explained by supposing that a part of the organic force is exhausted in balancing the material changes produced by the stimulus. But exhaustion also ensues when the action of an organ is increased without any external stimulus, if the organic force is not increased at the same time. It appears, therefore, that the very action of organs produces a change in their composition. It may be that the constant change which is produced in the organic substance by the action of the arterial blood, and which is as necessary to life as the decomposition of the burning matter is to the phenomenon of combustion, is accelerated or increased by the action of the organ, while the renovation from new nutritive matter does not take place with proportionate rapidity, and can only be effected gradually during rest. Generally, however, the more exertion a man uses, the more active seems to be the decomposition of the matters in his body, and the more need has he for nutriment. Both men and brutes that have died after very violent exertion, as in the instance of a stag hunted to death, undergo putrefaction much sooner than animals bled to death. Autenrieth,† who makes this remark, also instances, that a muscle taken from an animal before irritability had ceased, putrefies much sooner if stimulated to frequent contractions,

* Autenrieth's Physiol. i. 63.

† Physiol. i. 115. See also Humboldt über die gereizte Muskel und Nerven-fäser.

than if left at rest. In the functions of the nervous system especially, rest is so necessary, that even a life the most tranquil requires sleep, which comes on even while the causes which excite the nervous system to action, namely, the external stimuli, are in operation; the nervous system being rendered insensible to these impressions by reason of the change induced in it by its state of activity.

The constant reanimation of the tissues by the general vital stimuli ordinarily renders them capable of a proportionate exercise of their functions; but if their action is increased and accelerated, subsequent rest is necessary to restore as much power for new action as has been thus consumed.

Exercise.—Generally, in the healthy state, just as much power is generated in a certain space of time as has been exhausted by the exercise of the functions; but there are cases in which the nutrition of the organ becomes gradually increased while the state of action is either equal and regular, or alternating with rest. This is the case, for instance, in youth, because the affinity of the tissues for the vital stimuli seems, for reasons already stated, to be greater when the developement is less complete: indeed, *cæteris paribus,* the power of an organ is always increased by exercise, not carried too far, and alternating with rest; while mere rest often weakens an organ. This alternation of exercise and rest is the means by which a gradual increase of strength is to be acquired. Life generally is attended with decomposition of organic matter; in the same way, perhaps, the action of an organ is attended with decomposition of a part of its material, while another part becomes more intimately combined, so that, although an organ really loses matter by its state of action, still the same action renders it more capable of attracting new material and of strengthening itself. But when the action is repeated too frequently and violently, the renovation of material is even less, and exhaustion ensues. This is the case when the vital force is consumed, or rendered inert, by increased action, more quickly than renovation can be effected. The exhaustion is so much the greater, the more numerous and the more important the parts of which the action is thus frequent and violent, as, for example, in coitus, in which nearly the whole nervous system is thrown into a state of activity, attended with consumption of vital force; and the more the action of the organ is attended with a loss of something which it imparts to another part, as seems to be the case in the action of the nerves; and, lastly, the more the action of the part is attended with a real loss to the whole system, as in the case of increased secretions, for example, of the milk. The momentary state of inertness of the vital force after action, and its gradual restoration, is seen even in parts of frogs separated from the body; the irritability being restored probably by the action of the blood still con-

tained in the part, as well as by that of the air on the tissues. Thus the repeated application of galvanism to the leg of a frog separated from the animal exhausts its irritability, which is again restored after a certain interval of rest.

If an organ is very rarely called into action, its power is not restored by rest in the same degree as when it is subjected to more frequent exercise. The eye, for example, requires rest after being in action; but by alternating exercise and rest it is strengthened. If the eye is kept long in complete rest, it will have acquired great sensibility; but the vital force will have become weaker in proportion to the time that it has been left without exercise; and a strong impression of light will be sufficient even to blind an eye which has thus been kept long in darkness. Muscles lose much of their motor power by want of exercise; the power of the muscles of the ear, for instance, is lost for want of being exercised.*

Reaction.—Hitherto change in the organic activity of animals has been considered merely in a general manner. The operation of external influences in producing change in this property of animals shall now be investigated. The external "vital stimuli" are not the only agents which give rise to vital actions; everything which disturbs the elementary composition of organs, and the balance in the distribution of imponderable matters in the organic tissues, may also modify the action of the organism and of the separate organs. Such a modification when considerable is called *reaction;* the influence which produces this reaction in the organism is called *irritation;* and the cause exciting this irritation, the *stimulus* or *irritant.* The reaction is always a vital phenomenon, a manifestation of an organic property of the animal system. The property of reaction, of being excited to the manifestation of some inherent power on the application of an external influence, is not confined to organic beings, and still less to animals. Light or warmth are developed from many inorganic bodies, under certain circumstances, for example, by a blow. In these cases it is probable that the light and caloric existed in the bodies in a combined state, and are set free by the action of the external influence. A still better instance is afforded by elastic bodies, the minute particles of which have such an attraction for each other, that an attempt to displace a portion of them acts upon the whole; and by the power of attraction between them a *restitutio in integrum* ensues, accompanied with the phenomena of elasticity or sonorous vibrations. But no inorganic bodies are so uniform in their mode of reaction as the organised bodies, which, under disturbing influences, however various, always manifest the same phenomenon,—that, namely, with the capability for which each organ is endued by life. The uniformity in the mode of reaction of organised bodies arises probably from

* Autenrieth, Physiol. i. 104.

that fundamental property resident in them, of counterbalancing disturbances in their composition, by a force which, in the healthy state of the body, is much stronger than the disturbing cause. The force which restores the balance in the composition of the tissues after such a disturbance, is identical with that which preserves all the properties of a part during the constant process of nutrition and renovation of material. The phenomenon which ensues on the restoration of the balance, is constituted partly by the change produced by the external cause, and partly by the effort exerted to restore the balance. Dutrochet* maintains that all stimulants produce the same change in the organism,—that they modify the state of oxidation of the organic matter on which they act; the stimulant, he says, acts simultaneously on the oxygen and the organic matter, causing them to unite. Ingenious as this theory is, it is at present a mere hypothesis; as is also the conclusion that Dutrochet comes to, namely, that excitability is really a state of susceptibility of oxidation.

Irritation of an organ must always be attended with some material change in it. Such a change indeed must be presupposed even in the effect of the stimulus of light upon the eye. Light appears to enter into the composition of many bodies, and produces chemical changes, which are evident in several chemical preparations, and even in plants, in which light causes the developement of oxygen. The immediate effect which a stimulus produces, varies with the nature of the stimulus and of the body irritated; thus, it may be compression or a chemical change. But the secondary effect—the effort to counteract the former—is quite independent of the nature of the stimulus, is not mechanical or chemical, but is a manifestation of the vital property of the organ, such as sensation, manifested by pain, or inflammation, or spasm. Caloric, electricity, and light are imparted to organised beings according to the general laws of physics; but in the "restitutio in integrum" there always arises, at the same time, a vital action, which differs in its kind according to the part that has undergone the change; and the phenomena observed, until the part is restored to its natural state, are compounded of the operation of the stimulus and the reaction which it has excited. Chemical substances also produce a change in organic bodies, and have a tendency to form binary compounds with their elements. If this occurs,—if the organic affinity is not able to counteract the chemical agency,—a chemical product is formed, at the same time that the life of the part is destroyed, as is observed in the case of burns, and of the application of mineral acids or a caustic alkali. But the organised structure, thus acted upon by a chemical agent, while it retains its life, and on the boundaries of the part after its death, manifests the organic properties peculiar to it, such as sensation, motion, or inflammation.

* Froriep's Notizen. 724. Séances de l'Acad. d. Sc. Jan. 30, 1832.

The reaction of animal bodies on the application of external stimuli is peculiar, not merely in being manifested by vital properties, but these vital properties are frequently different, according to the nature of the organ and of its composition. Thus, for example, mechanical, chemical, or electrical stimuli applied to a muscle, all produce in it the same mode of reaction, namely, motion. So, also, all the different stimuli applied to a sentient nerve, excite sensation merely; and the kind of sensation is very different in different nerves, when the exciting cause is the same, and the sensation produced in the same nerve is always the same, although the exciting causes be different. Thus, for example, mechanical and electric stimuli excite, in the optic nerve, the perception of light, which is the peculiar property of this nerve, and seem to excite no pain; while pain, and not the perception of light, is the constant result of irritation of a sentient nerve. In the same way, mechanical and electric stimuli produce in the auditory nerve the perception of sound, and electricity excites in the olfactory nerve the sensation of smell. The anterior roots of the spinal nerves when irritated mechanically or by galvanism, give rise to no sensations, but to muscular contractions; while the posterior roots of the same nerves, under similar circumstances, excite sensations only, no contraction of muscles. By knowing the mode of reaction peculiar to all parts of the body, physiology acquires an empirical knowledge as certain as any possessed by the other natural sciences.

In perfectly different diseased states of the same organ the symptoms are often very similar; for in a state of excited action, as well as in a state of irritation with diminished power, the organ will manifest the vital properties peculiar to it. There are certain groups of cerebral symptoms, and of symptoms of cardiac disease, which occur in very different morbid conditions of each of these organs respectively. We may here remark upon the folly of the homœopathists, who imagine that they can cure diseases by means of substances which shall produce states of the system resembling the diseases; while they either do nothing whatever, or nature applies the remedies otherwise than the homœopathist imagines. The fact of two substances producing similar symptoms in one organ does not prove that these substances produce exactly the same effects, but merely that they act on the same organ, while the essential actions of the two may be very different. Syphilis, and the mercurial disease, may be essentially very different, and yet they so far resemble each other that certain organs are affected by both. Mineral acids and alkalies, also, are equally destructive to the organised tissues, and nevertheless no one will assert that they are "*similia*." In the same way, mercury, by inducing a slight change in the organic matter of the body, may render it unfit for propagating the destructive process of syphilis; and then the natural vital process, and not the mercury, effects the further cure.

The action of an organ being excited by stimulants, and every increase

of action without simultaneous increase of organic force being attended with exhaustion of this force, stimulants themselves must exhaust, or, as it were, consume the organic power; and unless, as in the case of the general *vital stimuli*, they have at the same time a restorative action, a temporary cessation of the action they have themselves excited will follow, although their influence is continued. Hence the periodic character of many vital phenomena. A contractile organ, containing a matter which stimulates it mechanically or chemically, contracts. By this act of contraction the part is rendered incapable, for a moment, of again contracting with equal strength; but the excitability is gradually restored, and the stimulus, which is constant, becomes again effective; and so the contractions are repeated from time to time. This intermittent action is seen in the undulations of the iris under the influence of an equable light, in the periodic contractions of the rectum, intestines, stomach, heart, uterus, urinary bladder, and of the muscles which expel the contents of the urethra in coitu. The stimulus to contraction is, in these cases, frequently external,—a substance contained in the cavity of the organs, such as urine, fæces, &c. It appears, however, also to be frequently internal, for instance, to be derived from the nerves, as in the case of the heart; the rhythmic contractions of which appear to be attributable to nervous influence, and not to the stimulus of the blood in its cavities, for the contractions continue when the organ is cut from the body and empty of blood; and in this case the stimulus of the blood is not supplied by the air, for the action continues in a vacuum.

A stimulus, too often repeated, deadens the excitability of the organ, and renders it insensible to the same stimulus for a long time. Hence may be explained a part of the phenomena observed in the effects of habit; although many things which produce this insensibility by repetition, produce not merely the phenomena of excitement at first, but a durable structural change, whence alone the subsequent inefficiency of these stimuli can be explained.

Classification of medicinal agents.—As the modifications produced in the composition of the organised tissues by the numerous agents and substances to the influence of which the organism is exposed are so various, —the modifications varying according to the nature and composition of these agents and substances,—and as we are unable to determine the nature of each modification, it is impossible to bring the substances used in medicine under a general good arrangement. Viewing them generally, however, there can be but three principal modes of action, and three classes of agents.

1. *Stimulants.*—The true and most important stimuli are the vital stimuli themselves, the constant operation of which on the tissues is alone the cause of the manifestation of life, and of the increase of the

vital force.* The vital stimuli are, a certain degree of external heat, atmospheric air, water, and nutriment. These agents do not merely produce a change in the composition of the organic structures and stimulate by disturbing the balance in the system, but renovate the tissues by entering, in a manner indispensable to life, into their composition. These influences, which are constantly in action, and which, while they stimulate, leave no exhaustion after them, are the only efficient means for restoring the powers of the body after an illness. There are many other stimuli which excite reaction, but which are not essentially renovating, and indeed for the most part have no restorative action on the organs; and which, except in producing symptoms or phenomena of reaction, have no vivifying influence; but, on the contrary, are injurious in proportion to the change effected by them in the organic composition. An endless injury has been done to medicine, and many lives have been lost, through the error of confounding all agents which excite reaction in the system with those which are absolutely essential to life, and which renovate while they stimulate the organs; the false notion having been thereby induced, that, because certain stimuli feed as it were the flame of life, stimulating agents generally are necessary to life. There are however some agents, in addition to the general vital stimuli, which under certain conditions exert a local, vivifying, and strengthening influence; they produce this effect by restoring the composition of the organ by their ponderable or imponderable influence, or by so changing its composition that the renovation by the general vital stimuli is facilitated. All this, however, depends on the state of the diseased organ; and the cases in which the so-called stimulant and tonic remedies have really their supposed effect, are very rare. While, on the other hand, many patients have been stimulated to death by a host of remedies which, under the circumstances of the case, or in all cases, stimulate, it is true, but only produce a tumult in the system, and do not strengthen it. Those substances which under certain conditions have a vivifying influence, also act principally, according to their composition, on different organs, and form natural groups according as their principal action is on the nervous system or on the organs destined to effect changes in the blood. Several of these agents are imponderable matters, such as electricity, which has been used with success in paralytic affections. Caloric, that agent which is necessary in the developement of the embryo, has also an eminently vivifying influence, when other means are fruitless; for instance, in affections of the nerves and spinal cord,—paralyses, neuralgia dorsalis, and commencing tabes dorsalis; the application of heat being made, for example, in the form of moxa, and frequently repeated, even by a new moxa on the old granulating surface: the application of

* See section 2. p. 29.

a single moxa is mere trifling. A much more durable impression of heat, better than moxa or actual cautery, is produced by holding a burning candle near to the affected part for a long time, so as to produce pain; by which means all the beneficial effect of heat is obtained, without the formation of an eschar and the subsequent suppuration, which is often of no service. The mode in which the caloric acts in these cases, is not evident; moxas are beneficial in diseases of the spinal cord, only when applied close to the spine, while pain may be excited in any part of the body.

Mechanical influence in frictions acts under certain circumstances as a vivifying stimulus; it has this effect, probably, by inducing, in the composition of the tissues, slight chemical changes, as a consequence of which the affinity of the tissues for the general vital stimuli already in the organism, is increased.

On the other hand, all agents of this kind, as well medicinal substances as caloric, electricity, and mechanical influences, such as pressure, contusion, &c. may, when their action is excessive, have the very opposite of a vivifying effect, by producing such a violent change in the organic matter, that the combinations necessary to life cannot be maintained: hence these influences are special stimuli, vivifying only under certain conditions. They exert a vivifying influence when their action on the organic matter favours the production of the natural composition of the parts. They may, therefore, be termed *homogeneous stimuli;* while all other stimuli, which only disturb the natural composition of the body, and thus the state of the vital powers, may be termed *heterogeneous stimuli:* these have no vivifying influence, but rather an injurious influence on life. It must however be remembered that every homogeneous stimulus, when used under improper circumstances, becomes a *heterogeneous stimulus.* The stimulants thus would seem to be divisible into, 1. the general vital stimuli; 2. the special stimuli; and these again are divisible into *a*, the homogeneous, and *b*, the heterogeneous. I have already mentioned that Dutrochet supposes the true stimuli to act by favouring and accelerating the combination of oxygen with the organic matter. It is probable that the action, at least of several stimuli, depends on their having the property of strengthening the affinity between the organic substance and the blood, (which, by its passage through the lungs, is itself rendered a vital stimulus,) and thus of increasing and accelerating the changes produced in the organic matter by this principle (oxygen) in the blood.

In cases of rapid sinking of the vital force, all our stimulant remedies are of no avail; and the greater part of such remedies merely excite the system, and do not add to the strength.

2. *Alteratives.*—A great number of substances are important as medicaments, from producing a chemical change in the organic matter, of

which the result is, not an immediate renovation of material and increase of vital force, but the removal of that state of combination of the elements which prevented healthy action, or excited diseased action; or the chemical change produced is such as to render the organ no longer sensible to a morbid stimulus; or it is such that certain apprehended destructive changes in its composition are no longer possible, as in the antiphlogistic plan of treatment; or, lastly, these substances produce a change in the nutritive fluids. Such substances are alteratives. By these remedies an organ morbidly changed in composition cannot be rendered sound by, as it were, a chemical process, but such a slight chemical change can be produced as shall render it possible for nature to restore the healthy constitution of the part by the process of nutrition. These remedies again may be divided into two principal kinds, according as they act chiefly on the nervous system or on the other organs dependent on that system. Among those of the first kind the most important are the so-called narcotics; those of the latter kind comprehend the numerous medicines which exercise their action on diseases in other organs. These remedies also, by removing the obstacles to cure, become indirectly vivifying or renovating stimuli, and they may themselves, by disturbing the balance in a part, produce symptoms of irritation. If used in excess, they either give rise to the injurious effects of the heterogeneous stimulants, or, by inducing a sudden change of composition, annihilate the vital force, as is the case with the narcotics. Since, however, such alterative medicines affect the composition of an organ each in its own way, one alterative may, after a time, lose its influence, as it were, from saturation, while the organ may still be susceptible of the influence of another. A great number of the instances of habituation are referrible to this cause. The administration of medicines affords, in innumerable cases, the confirmation of this statement. By the continued use of an alterative medicine, the composition of the organ shall have suffered such a chemical change, that the same affinity for this substance no longer exists in the organism, while an affinity for another substance may still remain. Imponderable matters also are in this way alterative; thus the eye, after being long fixed on a green surface, becomes gradually more and more insensible to this colour, which becomes dull and grey. At the same time, however, the sensibility for the red rays is increased, and a long exposure of the retina to the red rays makes it susceptible of the green. In the same way, by fixing the eye long on yellow, the sensibility for that colour is lost, while the perception of violet becomes more intense, and vice versâ; the same relation exists between blue and orange.

3. *Agents which destroy the organic composition.* (Zerzetzende mittel.) —These are influences which, without first producing a stimulant or simply alterant effect, directly destroy the essential composition of the

organised tissues. Some of the agents which are stimulant when they operate gently, produce by a more violent action too important a disturbance of the powers of the part; such are heat, electricity, &c. Others are *alteratives*, which by an extreme degree of their action produce great changes in the composition of the tissues, forming with organic matters combinations which the organic force is not able to counterbalance; it is in this way that the *narcotic alterants* have a destructive action; and those alterants which modify the formation of the fluids of the body and the organic changes effected in them by different organs, —for example, the antimonial and mercurial preparations, and the mineral acids and alkalies,—have, when in a concentrated state, an equally destructive influence on the organic composition. Stimulants can produce disorganisation in two ways. They may, in the first place, be stimulants only when their action does not surpass a certain degree of intensity; and, when their action is more violent, they may, instead of renovating the material, or even favouring this renovation by exciting new affinities, produce immediately an essential change of composition. In this case no irritation or reaction precedes the local or general death; the disorganisation is immediate, as in death from electricity, lightning, &c. Or, secondly, a stimulus, which under certain conditions has a renovating action, may have a destructive effect by exciting the action of an organ during too long a period; more force being exhausted than can be restored again in an equal space of time. This action is called over-excitement. An organ thus over-excited, as, for example, the eye by light, is rendered permanently weaker. The agents here referred to are used in medicine only when it is wished really to produce destruction of a part.

Theories of Brown and the Contra-stimulists.—John Brown, who, by the discovery of some of the laws of excitability, was enabled to give in his "Elementa Medicinæ" the first hint for a scientific system of medicine, but in a crude, and, for application to practice, dangerous form, was as little acquainted as his followers with the mode of action of alterative medicines. According to Brown's theory, no change can take place in the state of the excitable powers without previous excitement; and it is only by over-excitement that the excitability, with life, can be exhausted. The Brunonians were obliged to maintain, that, whenever exhaustion was produced by any influence, absolute over-excitement had preceded this exhaustion. As proof of this assertion, they adduced the circumstances that many substances administered in small quantity stimulate, in larger quantity produce quite a different state, and in still larger quantity cause exhaustion: opium was their example. In the last case, when exhaustion is produced, the period of excitement is extraordinarily short and imperceptible. They explained the action of all agents which rapidly produce exhaustion in the same manner. But there are many substances which, even in small quantities,

produce these disorganising effects in a slighter degree; such are the irrespirable gases, the poison of the viper, &c. The *contra-stimulists*, Rasori, Borda, Brera, and Tommasini, perceiving this defect in the Brunonian theory, gave the name of *contra-stimulants* to those substances which, in place of stimulating, have the very opposite effect, — that is to say, diminish the excitability of parts; so that they have divided their medicines into the stimulants and contra-stimulants: but, although they have not overlooked this great error of Brown, they have failed to recognise that alterative action of many medicines which has been pointed out in the preceding pages.

The distinctions made by Brown originate in a very partial application of some well-grounded laws of excitability, and in the error of confounding the renovating vital stimuli with substances which modify the action of organs and their healthy composition, and which in that respect stimulate, but do not renovate at the same time. A narcotic—that is, an alterant of the nervous system,—may from the commencement to the end of its action produce symptoms; by changing the organic composition, it acts upon that fundamental property of the organism by which external influences determine them to action in accordance with internal laws, or, in other words, stimulate them. But this is not a stimulant in a therapeutic sense; by which is understood an agent which vivifies the organs, and renovates their composition.

John Brown divided diseases into the sthenic and the asthenic. In the former, he supposes the vital force to be increased; in the latter, diminished. But a disease with increased vital power involves a contradiction; and diseases present merely an endless variety of defects in the composition of organs, in which the general forces at one time fail from the very beginning; at another time, are present at first, but afterwards diminish: the best mode of arranging diseases, therefore, is founded on the different systems of organs affected, and the types of disease established by their natural history. Physicians have always been inclined to regard inflammation as a disease with increased vital power: but it is in reality a disease in which certain properties of the body are undoubtedly increased,—for example, the heat;—in which the quantity of the blood in the capillaries is greater, but in which other conditions of the part are altered; while the function of the organ is interrupted, and the sensations indicate a violent lesion. The exciting cause of inflammation produces a chemical change in the composition of an organ; it is in this way produced in the practice of medicine by chemical agents. A chemical affinity, an attraction, may arise between the blood and the tissues thus chemically changed. This affinity may be greater than in the healthy state. But whether the increased affinity between the tissue and the blood in inflammation be merely a greater degree of the natural organic attraction, such as is observed in certain

healthy phenomena, as in all the phenomena of turgescence, — or whether it is essentially different from the organic attraction, and is a newly arisen chemical affinity between the disorganised matter and the blood,—cannot with certainty be determined. But even if the increased affinity between the blood and the organic substance be really a greater degree of that reciprocal action which is constantly going on between the blood and the tissues, still inflammation is not a disease of increased vital power; for the phenomena of inflammation arise as much from the existing tendency to decomposition excited by the chemical change, as from the reaction of the tissues to oppose this destructive tendency.

The intimate reciprocity of action which exists between all parts of the organism, especially through the medium of the nervous system, produces in animal bodies a kind of balance (statik) of the forces; whence it results, that an exciting cause of disease acting on one part, by changing the state of the ponderable and imponderable matters, often exerts its influence through a chain of such changes on distant parts, which are most susceptible of this form of disease. It is not merely that the withdrawal of matters at one point prevents the accumulation of similar or different matters at another spot, on which is founded the use of evacuating means at parts of the body distant from the disease; but the increase of vital action in one organ excites many others: hence the connection of the increased vital action in the genital organs with the reproduction of the antlers in the stag, and with changes in many organs in man, which changes, both in the stag and in man, are prevented by castration. The application of renovating stimuli, also, to one part, has a vivifying influence on the whole system, reacting from the skin, for example, on the central organs of the nervous system through the medium of the nerves; whence arises the successful use of frictions, and other stimulants to the skin, for the restoration of suspended animation.

4. *Of the phenomena, or active properties common to inorganic and organic bodies.*

Organic bodies participate in the general properties of ponderable matter. The laws of mechanics, statics, and hydraulics, are also applicable to them. Several of these properties which organic matters may possess in common with inorganic substances, such as cohesion, elasticity, &c. exist, however, only while the essential composition of the part is maintained by the continued operation of the organic force; thus the elastic coat of arteries loses its elasticity soon after death. The application of the laws of mechanics, statics, and hydraulics to the actions of organic bodies is also limited, from the circumstance that the causes of motion most engaged in them are essentially vital in their nature.

The imponderables, also, namely, electricity, caloric, and light, are developed by organic bodies. It is these matters that we must here particularly consider.

1. *Developement of Electricity.*

Sources of electricity.—The electricity excited by friction is well known to be developed more especially from many substances of organic origin: galvanism, or the electricity of contact, is not produced merely by the contact of heterogeneous metals; many other substances, particularly carbon and graphite, may, as has been shown by Humboldt and Pfaff, supply the place of metals; and even many animal substances connected by conducting bodies will produce in a less degree the same phenomena as metals of different kinds. It would, therefore, be quite erroneous to suppose that the causes of galvanism are to be sought only in the properties of different metals. Seebeck has discovered that even bars of the same metal heated to different degrees of temperature, and placed one upon the other, will become electric; and that one simple metallic bar made of a different temperature at the two ends has the same property: so that different quality of the parts coming in contact (by throwing the electricity which is present in all bodies into the state of positive and negative electricity, or by disturbing the balance of the electric matter,) together with connection by means of a conducting substance, seem to be the most general conditions required for the production of galvanism. Galvanic phenomena are also produced in the parts of animals under these circumstances. The Baron von Humboldt discovered that feeble contractions are produced in the leg of a frog by touching the nerve and muscle at the same moment with a fresh portion of muscle. This is certainly one of the more rare results of galvanic experiments; but I have repeated the experiment several times, and can confirm the accuracy of the result. Buntzen indeed formed a weak galvanic pile with alternate layers of muscle and nerve; and Prevost and Dumas state that a circle formed simply of one metal, fresh muscle, and a saline solution or blood, affects the galvanometer. If to the conductors of the galvanometer, plates of platinum are fixed, and a piece of muscle of several ounces' weight placed upon one of these plates, the conductors being then immersed in blood or a saline solution, a deviation of the magnetic needle of the instrument takes place. Or if to one of the conductors, a piece of platinum moistened with muriate of ammonia or nitric acid is attached, to the other a portion of nerve, muscle, or brain, and the two conductors made to communicate, the same deviation is produced.* Kaemtz† has moreover shown, that dry but efficient galvanic piles can be constructed from organic substances without any concurrence of metals. Concen-

* Magendie's Journ. t. iii. † Schweigger's Journ. 56. 1.

trated solutions of organic substances were spread upon thin paper, and with disks of this paper piles were constructed, the two layers of different substances being separated by two thicknesses of paper; the electricity developed by these piles was tested by an electrometer (Bohnenberger's). It was by this means ascertained that

Soda	is positive with reference to	Mutton fat.
Yeast	. . . .	Cane sugar.
Yeast	. . . .	Common salt.
Yeast	. . . .	Sugar of milk.
Linseed oil	. . . .	Sugar.
Linseed oil	. . . .	White wax.
Starch	. . . .	Gum.
Gum	. . . .	Saloop.
Gum	. . . .	Mucus of tragacanth.
Gum	. . . .	Seeds of lycopodium, (barlappsamen.)
White of egg	. . . .	Gum.
White of egg	. . . .	Bullock's blood.
Bullock's blood	. . . .	Extract of belladonna.
Bullock's blood	. . . .	Starch.

These facts being known, the electric fishes appear less extraordinary, although their power of producing electric discharges exists only during life, and during an undisturbed state of the nervous influence. The electric fishes which are best known are the electric ray, or torpedo, of which the species ocellata and marmorata occur in the seas of the south of Europe; the electric eel, gymnotus electricus, which is found in several rivers of South America; and the silurus electricus, or malapterurus electricus, met with in the Nile and in Senegal. The rhinobatus electricus, trichiurus electricus, and tetrodon electricus, are less known. Walsh, Fahlenberg, Gay Lussac, and Humboldt, have contributed most to our knowledge of these fishes.

The electric organs of the torpedo lie on each side of the head and gills, and consist of a number of five or six-sided prisms placed perpendicularly side by side, and occupying the whole thickness of the fish. Each prism consists of a tube with thin membranous parietes, surrounded with nerves and vessels, and containing a great number (one hundred and fifty) of extremely thin lamellæ, lying transversely, parallel one above another, with a gelatinous fluid in the intervals. Three large branches of the vagus nerve are distributed to these organs on each side, branches being previously given to the branchiæ. A branch of the fifth nerve also is distributed to the anterior part of each organ.* The electric organs in the gymnotus and silurus are described by Rudolphi to extend from the head to the tail, two on each side; one of these is situated deeply, and one superficially, the two being separated by a septum, and in the gymnotus, at the sides, by muscles also. In the

* Hunter, Philos. Trans. 1773, p. ii. tab. 20.

gymnotus electricus the organs are formed of horizontal membranes extending longitudinally, one-third of a line distant from each other, with septa passing perpendicularly between them and running from within outwards, the spaces between these septa containing a fluid. The smaller deeply seated organ is still more finely divided. The nerves are two hundred and twenty-four intercostal nerves, which descend at the inner side of the organ and distribute branches in each layer; the minute terminations of the intercostal nerves themselves passing under the small organ to the skin. A nerve, composed of branches of the fifth and vagus nerves, passes superficially, and is distributed to the muscles of the back without giving branches to the electric organs.*

In the silurus, Rudolphi ascertained that there are also two electric organs on each side; the following account of them is derived from my own observation, as well as from Rudolphi's description. The two organs are separated by an aponeurotic membrane; the external one lies superficially under the skin, the deeper one immediately upon the muscles; the nerves of the external organ are derived from the nervus vagus, which runs under the aponeurosis, and sends branches through it to reach the organ. The nerves of the internal organ are derived from the intercostal nerves, and are very minute. The external organ consists of very small lozenge-shaped cells, which it requires a lens to see: the internal one seems also to be formed of cells. Rudolphi calls the substance of the internal organ flaky.†

The effects produced by the electric fishes on animals are perfectly analogous to electric discharges. The shock from the torpedo when the fish is touched with the hand reaches to the upper arm. The gymnotus will attack and paralyze horses even, as has been so well described by Humboldt. Substances which are conductors or non-conductors of electricity bear the same relation to the influence communicated by the torpedo and the gymnotus, which are the only electric fishes that have been hitherto accurately examined with reference to their electric action; and a shock is propagated through a chain of several persons when those at the extremities of the chain touch the fish. Walsh has indeed obtained sparks by conducting the discharge of the gymnotus through a strip of tin foil which was gummed to a piece of glass and cut through in the middle; it was at the line of the section that Walsh, with Pringle, Magellan, and Ingenhouss, saw the spark pass from one half of the foil to the other.‡ Fahlenberg has repeated this experiment with the same result, while the fish was exposed to the air.§ Not the slightest action had ever been observed to be produced either by the

* Rudolphi in den Abhandlungen der Academie von Berlin, 1820, 1821, p. 229, tab. i. ii.

† Rudolphi in Abhandl. der Acad. zu Berlin, 1824.

‡ Journ. de Phys. 1776, Oct. 331.

§ Vetensk. Acad. Abhand. 1801, ii. p. 122.

torpedo or by the gymnotus, on the electrometer, by Humboldt and Bonpland, Gay Lussac, or Sir H. Davy. But Dr. John Davy has discovered that the electric organs of the former fish really have an electric action on the galvanometer. [Dr. Davy* also ascertained clearly that the electric discharge of the torpedo will render needles magnetic. This has been confirmed by Linari,† who, as well as Matteuci, has obtained sparks, decomposed water, and observed marked deviations of the galvanometer at the moment of the discharges.]

Laws which regulate the discharges.—The power of producing the discharge is quite voluntary, and dependent on the integrity of the nerves of the organs. The heart may be removed, and the shocks will still be communicated for a long time; but with the destruction of the brain, or division of the nerves going to the organs, the power ceases. The destruction of the electric organ of one side does not interrupt the action of the opposite organ. All observers agree, that the electric discharge does not take place every time that the fish is touched, but depends on a voluntary power, so that it is often necessary to irritate the fish. Moreover, it would appear that it has the power of determining the direction of the discharges; for when Humboldt and Bonpland laid hold of the fish, one by the head, the other by the tail, the shock was not always felt immediately, and both did not always receive it. Sometimes the animal struggles when teased, without giving any shock. It seems to be itself scarcely sensible of the shocks. In the electric eel no motion is observed at the time of the discharge, and in the torpedo there is merely a slight motion of the thoracic fins; while the electric fishes are very sensible to the artificial galvanic stimulus applied to wounds. No convulsive motions, however, are produced in the gymnotus, according to Humboldt's observation, when one of these fishes receives a shock from another.

The electric shock is felt, if the animal is inclined to communicate it, by merely touching one surface with a single finger, as well as by applying the hand to both surfaces, dorsal and ventral. In either case it is a matter of indifference whether the person, who touches the fish, is isolated or not. Dr. John Davy,‡ however, states that the dorsal and ventral surfaces have different electric properties; [that the electricity of the dorsal surface is positive, that of the ventral surface negative; and that unless both surfaces are touched, no shock is felt. Matteuci || also, who had the opportunity of instituting experiments on a great number of these fishes, could detect no current by means of the galvanometer, when both plates connected with the wires of the instrument were placed upon the back, or both upon the belly. While, when one wire was connected with the back, the other with the ventral surface,

* Philos. Trans. 1832.

† Séances de l'Academie des Sciences, Juillet, 1836.

‡ Phil. Trans. 1834.

|| Séances de l'Academie des Sciences, Octob. 1836.

whether both wires were applied on the same side, or one on the right side the other on the left, a current was detected passing from the dorsal to the ventral surface, the dorsal surface being positive, the ventral negative. These currents, however, were not perceptible at any part of the body except during the discharges. The experiments of M. Colladon,* who had more than forty torpedos at his disposal, seem to explain the discrepancy in the statements of different observers as to the possibility of perceiving the shocks when one surface only of the body is touched. The results M. Colladon obtained with reference to this point are the following. The dorsal surface throughout is positive, when it is connected with any part of the ventral surface; and the electric action is weaker the more distant the part is from the electric organ. When the wires are applied to two symmetrical points of the back, no effect is produced upon the galvanometer. But when the two points on which the wires are placed are not symmetrical, whether they be both on the belly or both on the back, a current is detected by the galvanometer, a deviation sometimes of 20° or 30° being produced, the part nearest to the organ giving positive or negative electricity according as it is on the back or on the belly.]

In many respects the torpedo and gymnotus agree; in a few they differ. Gay Lussac and Humboldt have remarked some interesting points of difference. When the torpedo is touched with a single finger, the discharge takes place, whether the person is isolated or not. But when he is isolated, the contact with the fish must be immediate. If the torpedo is touched with a piece of metal held in the hand, no shock is felt; while the gymnotus transmits its electric discharge through a bar of iron several feet in length. If a torpedo is laid upon a very thin plate of metal, the hand which holds the plate never perceives the shock, even though the fish be irritated by another person who is isolated, and though the spasmodic movements of the thoracic fins indicate that strong discharges are taking place. If, however, the torpedo, lying on a metallic plate, which is held as before with one hand, is touched on the upper surface with the other hand, a powerful shock is felt in both arms. The sensation is the same when the fish is between two metal plates, the edges of which do not touch each other, and when the hands are placed at the same time on the two plates. But when the borders of the plates are in contact, the shock ceases entirely to be felt; the circle between the two surfaces of the electric organs is completed by the metallic plates, and the new circle formed by bringing the two hands in contact with opposite plates, has no effect.

Electric fishes, which are still vigorous, exert their electric power as strongly in the air as in the water. If several persons form the chain between the upper and under surfaces of the fish, the shock is not felt

* Séances de l'Acad. des Sciences, Octob. 1836.

unless these persons have previously moistened their hands. The discharge, however, is felt by two persons, who, while grasping the torpedo with their right hands, complete the circle—not by holding each other by the left hands, but by each dipping a small bar of metal into a drop of water on an insulated body.* Lastly, it is to be remembered that Spallanzani observed, that the torpedo loses its power of giving shocks when its skin is removed. [Matteuci, however, states that the electric shock of the torpedo is felt when the skin is removed from the organ, and even when slices of the latter are removed. M. Matteuci thinks that the electric influence is derived from the brain, and is only strengthened in the organs as in a Leyden phial. He found the intensity of the shocks diminish in proportion to the number of the nervous fibres going to the organ, which he divided. Two grains of muriate of morphia introduced into the stomach, in ten minutes produce death, attended with convulsions and strong electric discharges. When the animal had ceased to give shocks, even when irritated, discharges stronger than ordinary, and following the usual course from dorsal to ventral surface, were excited by laying bare the brain and touching the posterior lobe from which the nerves arise. If, instead of simply touching the brain, wounds were inflicted on it in no certain direction, the shocks were renewed, but the electric currents followed no constant course; under these circumstances M. Matteuci observed three discharges in succession, which passed from the belly to the back.]

Electric phenomena in frogs.—The electric phenomena of the electric fishes are effected by means of special organs. Whether electricity is developed in animals by ordinary vital processes is another question. Electricity exists in all bodies in a state of equilibrium, and by contact of certain bodies can be made evident by being thrown into positive and negative states even in living frogs. In the spring before the time of breeding, and in the latter cold part of autumn, but not in the summer, frogs evince great sensibility to the galvanic stimulus. If at these times the leg of a frog, dissected in the usual manner, is laid upon a glass plate, and the crural nerve touched with a plate of zinc held in one hand, while the experimenter touches the leg with a finger of the other hand, a strong contraction of the muscles ensues every time the circle is thus closed; if copper is used in place of zinc, the result is the same, but the contraction is not so strong. I found also that if the nerve of the frog's leg was laid upon a plate of zinc, and the nerve and muscles of the leg then connected by a piece of the flesh of a frog, a contraction of the muscles was always produced. The effect was indeed the same, when the zinc plate on which the nerve lay was approximated to the surface of the limb. Lastly, having removed the thigh,

* See Gay Lussac et Humboldt, Ann. de Chemie, 65, 15. A. v. Humboldt's Reise in die Æquinoctialgegenden des neuen Continents. 3 Theil, pp. 295—324. Treviranus Biolog. vi. 144—180.

leaving merely the crural nerve attached to the leg, I brought this nerve, by means of an isolating rod, near the surface of the limb, and made it touch the moist skin of the leg; contraction of the muscles then took place both at the moment of contact and also at the moment that the nerve was separated from the surface of the limb. This experiment, which Humboldt had already performed in a different manner, is extremely remarkable, and is the simplest galvanic experiment which can be made on a frog. No metal is required, but the leg with the nerve hanging from it must lie upon a glass plate. The nerve is raised gently upon a quill, and turned back so as to touch merely the leg; a contraction of the leg, then, sometimes occurs. Another experiment, which I have made, is more complicated; it consists in closing the circle between the nerve of the dissected thigh and the surface of the leg, by means of two living frogs or two frogs' legs; even portions of a dead and putrefying frog may be used to complete the circle. If the nerve which hangs to the upper extremity of the frog's leg is laid in a saucer containing blood or water, it matters not which, and the fluid in the saucer is brought into connection with the muscles of the thigh by means of a copper wire, a muscular contraction is produced, equally as well as if the nerve itself and the thigh were directly connected by means of a copper wire, or a portion of fresh or putrid muscle. In the first experiment, in which I closed the circle between the nerve lying on a zinc plate and the leg, by means of my own body, I imagined that the contraction produced was excited by the electricity of my body. But when I saw that a dead frog or a piece of putrid muscle was equally efficient, and that muscular contractions could be produced by closing the circle between the ischiadic nerve and muscles of the thigh with copper wire and water, I immediately changed this opinion. Lastly, the experiment in which, nearly in the same manner as Humboldt, I excited muscular contraction by turning back the nerve towards the surface of the leg still covered with cuticle, without any intermediate conductor of metal or muscle, proves that for the simplest electric phenomenon on frogs, or separated parts of frogs, the mere contact of nerve and muscle, which at their other extremities are organically connected, is sufficient, and that the use of conductors of metal, or of fresh or putrid muscle, merely strengthens the phenomenon. It appears then, either that free electricity is generated in living bodies, and that when certain substances come into contact an overflow of this electricity takes place and produces muscular contractions, or that the mere difference in chemical properties of the nerve and muscle, produces an electric tension, while closing the circle restores the electric equilibrium and produces the contraction. All the phenomena above described are observed in frogs only in the spring before the breeding season, and in the cold part of autumn, either on account of the greater excitability or the greater accumulation of electricity at those times.

Explanation of these phenomena.—From the above experiments it appears, that the electricity which exists in dead and living animals, as in all other bodies, is under certain circumstances thrown into a state of tension, or, in other words, separated into positive and negative electricity. In the leg of the frog, the discharge takes place when the circle between the nerve and muscles, which are in different electric states, is closed. The thigh of the frog in this case acts the part of a most delicate electrometer, contraction of the muscles being produced by the electricity developed in it. It is uncertain whether the different electric state of the nerve and muscle under these circumstances is a result of the vital process, or arises merely from the electricity, which existed previously in a quiescent state in these parts, being, as in the phenomena of galvanism generally, thrown into a state of tension by the contact of heterogeneous substances: it cannot be ascertained whether a dead nerve and muscle are susceptible of this tension; for, even if it were produced in them, the dead muscle having lost its contractility would not indicate it. Much that is fabulous has been alleged concerning the developement of electricity during the vital process. The truth is, that the electric phenomena, which are manifested in animals independent of friction, are very feeble; although it does not appear possible for the various chemical changes, which take place in them, to occur without some developement of electricity.

Free electricity in man.—All that is known concerning the developement of electricity in the human subject under the influence of the vital process, is furnished by the researches of Pfaff and Ahrens.* The experiments were performed with the aid of a gold-leaf electrometer, the persons who were the subjects of the experiments being placed upon an insulating stool. The collector plate of a condenser, which was screwed upon the electrometer, was touched by the person, while the other plate of the condenser communicated with the earth. The results obtained are the following:

1. As a general rule, the kind of electricity evidenced by man in the healthy state is the positive.

2. It seldom exceeds in intensity the electricity excited when copper, which communicates by a conducting substance with the earth, comes in contact with zinc.

3. Excitable persons of a sanguine temperament have more free electricity than indolent persons of a phlegmatic temperament.

4. The quantity of the electricity is greater in the evening than at other periods of the day.

5. Spirituous drinks increase the quantity of electricity.

6. Women are more frequently negative electric than men, although there is no determinate rule for the prevalence of this kind of electri-

* Meckel's Archiv. iii. 161.

city. Gardini had found that women manifested negative electricity at the time of menstruation, and also during pregnancy.

7. In the winter, bodies, which are very cold, at first give evidence of no electricity; but it gradually becomes manifest as warmth is restored.

8. The body, when perfectly naked, manifests the same phenomenon, which is also common to all parts of it.

9. During the continuance of rheumatic affections, the electricity of the body seems to be reduced to zero, and to reappear as the disease subsides. It appeared to Humboldt,* that rheumatic patients had an insulating action on the feeble current produced by a simple galvanic circle.

Do any vital actions depend on electricity?—Much has been said of the production of several vital actions, particularly those of the nerves, by the agency of electricity. But nothing of this kind has been demonstrated. Neither Person† nor I have ever been able to detect electric currents in the nerves.‡ Pouillet at first thought that he had perceived electric currents in needles inserted into the flesh in the operation of acupuncturation; but he has himself acknowledged his error.§ Having inserted a needle into a diseased or healthy part of the body, and taken another needle into the mouth, he connected the conducting wires of the galvanometer with the two needles, and perceived several times soon afterwards oscillations of the magnetic needle; but I did not perceive this effect on the needle when I repeated the experiment. Pouillet, however, imagined that the electricity arose from the oxidation of the needles inserted into the flesh; for a very delicate galvanometer will indicate the oxidation of metals. In fact, not the slightest deviation of the needle took place when the needles employed were formed, not of steel, but of a metal which does not easily oxidise, such as platina, gold, or silver. In that case it is also possible for oscillation to be caused by the end of the needle inserted into the body being heated more than the other, which alone, it appears from Seebeck's discovery, would be sufficient to develope galvanic electricity in the needle.

Donni has recently discovered, by means of a very delicate galvanometer, that there is really an electric action between the inner and outer surfaces of the skin, which action he attributes to the alkaline and acid properties of the secretions.|| Matteuci has seen a deviation of the needle amounting to 15 or 20 degrees when the liver and stomach of a rabbit were connected with the platinum ends of the wires of a delicate galvanometer. He imagines that this action does not de-

* Humboldt, über die gereizte Muskel. und Nervenfaser, i. v. 159.

† Magendie's Journal de Physiol. x. 216.

‡ This subject is more particularly discussed in the Book on the Nervous system.

§ Magendie's Journal de Ph. v. p. 5.

|| Ann. des Sciences Nat. 1834, Fev.

pend on the difference of the chemical properties of the secretions, because it became very feeble, or entirely ceased, after the death of the animal. In the nerves themselves Matteuci could detect no electric action; but he also found that the nerves do not affect the galvanometer, even when the current of a galvanic battery is passed through them. Hence, even if there were really electric currents in the nerves, they would not be detected by the galvanometer.* Bellingeri has made some experiments on the electricity of the blood removed from the body that of the bile, and of the urine, from which he concludes that in inflamed blood the electricity is diminished, and that blood retains its electricity long after it has been abstracted from the body.† But how desirable it would be to prove first the real existence of free electricity in the blood generally!

Prevost and Dumas regard the microscopic flattened particles of the blood, consisting of a nucleus and capsule, as pairs of galvanic plates; and Dutrochet even endeavours to prove that the nuclei are negative electric, the capsules positive electric. This hypothesis will be refuted in the section on the Blood. Dutrochet's imagined formation of muscular fibre from the blood by the agency of electricity, will be shown to be equally an error. Several French physiologists, following Hunter, Abernethy, Prochaska and others, attribute every process in the animal body to electric action. In treating of the nervous system, I shall show, however, that although, as appears from my own experiments, electric actions can be generated in the nerves, still the mode of action of the nerves is wholly different from that of electricity.

Among modern physiologists, no one has carried the hypothesis of electricity being the cause of vital phenomena to a more extravagant length than the chemist Meissner.‡ With no proofs to support it, he advances the following hypothesis. He supposes that, during the chemical process of respiration, the blood becomes charged with electricity; that at the same time the electric fluid is distributed through the pulmonary nerves and the ganglionic system, and from them is communicated to the great nervous centres. He supposes further, that the brain, the seat of volition, being thus charged with electricity, excites the action of any desired organ by giving an electric spark to the corresponding nerve; that the electric fluid sent to the muscles forms an atmosphere around each of the molecules, which by their union in a linear form constitute a fibre, and thus forces asunder at their middle the muscular fibres, which being firmly united at their extremities, contraction of the muscle is produced, just in the same way as, when several

* Matteuci, L'Institut. Nr. 75.

† Experimenta in electricitatem sanguinis, urinæ, et bilis, Mem. d. A. d. Tor. v. 31.—Froriep's Not. 19, 177.

‡ System der Heilkunde aus den allgemeinsten Naturgesetzen. Wien, 1832.

threads, with a number of pith balls strung upon them, are tied together at both ends, hung upon an electric conductor and electrified, the individual balls and threads are forced asunder, and the two ends of all the threads are approximated. Independent of the known fact that muscular fibres while contracting do not separate from each other, but are thrown into zigzag flexures, there is not one single proof in support of all this visionary speculation. Meissner explains by his theory the cures effected by the so-called animal magnetism. But it ought first to be ascertained whether electricity is really developed in the processes of incubation, respiration, &c.

Pouillet has endeavoured to prove, that during the vegetation of plants, an abundance of electricity is developed. Pouillet first investigated the generation of electricity in the formation of carbonic acid. He placed a cylinder of carbon on the plate of a condenser, inflamed the upper end of the cylinder, and supported the combustion by a moderate current of air. In a few moments the condenser was charged with negative electricity, while the carbonic acid formed, coming in contact at the height of a few inches with a brass plate, which was connected with the condenser, was found to possess positive electric properties. In his experiments on the developement of electricity during vegetation, Pouillet made use of twelve glass vessels from eight to ten inches in diameter, which he covered externally for the extent of one or two inches near the border with a varnish of gumlac. These vessels he placed in two rows on a piece of very dry wood. He then filled them with garden-mould, and connected them by metallic wires, which passed from the interior of one vessel to that of another, so that the interior of all the vessels formed part of one circle. If, now, electricity was developed in them, it would be distributed through all the vessels, but would be prevented from escaping by the varnish at their margins. He now connected the isolated plate of a condenser with one of the vessels by means of a brass wire, while the lower or moveable plate of the condenser communicated with the earth. The apparatus being thus prepared, some seeds were sown in the earth contained in the vessels. In a few days resinous electricity was developed in the vessels, while vitreous electricity was detected in the gases formed. This continued until the air of the chamber became impregnated with moisture.* These experiments must be repeated with the necessary modification on incubated eggs, and on animals with reference to the formation of carbonic acid during respiration.

2. *Of the generation of Caloric.*

The temperature of the human body in those internal parts which are most easily accessible, such as the mouth and rectum, is 97·7° or 98·6°

* Annal. de Chim. et de Phys. 35, 420.

Fahr. The temperature of the blood is found to be from $100\frac{3}{5}°$ to $101\frac{3}{4}°$; Magendie states it at $101\frac{3}{4}°$; Thompson at 101°; in some diseases it is as high as from 106° to 107°. In the morbus cœruleus, in which there is defective arterialisation of the blood from malformation of the heart, the temperature of the body is often several degrees lower than natural; for instance, as low as 79° or $77\frac{1}{2}°$; in the Asiatic cholera, a thermometer placed in the mouth rises only to 77° or 79°. The temperature of the body in health is, according to Autenrieth, $1\frac{1}{2}°$ Fahr. lower during sleep than during the day, and somewhat lower in the morning than in the evening. In warm climates, Dr. Davy found the temperature of the interior of the body 2·7°—3·6° Fahr. higher than in temperate climates: he observed this difference of temperature in individuals of different ages, and in natives as well as in persons coming from cooler climates. This last observation is, however, quite opposed to the results of Douville's experiments.*

Temperature of mammalia and birds.—Tiedemann and Rudolphi have collected all the facts known relative to the temperature of different animals.

The following is derived from the more copious table of Tiedemann.†

The Ox has a temperature of from	99° to 104° Fahr.
Sheep	100·40° to 104°.
Horse	97° to 98·24°.
Elephant	$99\frac{1}{2}°$.
Guinea-pig	96·37° to 100·40°.
Hare	100°.
Rabbit	99·46° to 104°.
Squirrel	105°.
Seal	102°.
Dog	99·30° to 101·30°.
Cat	98·60° to 103·60°.
Bat.—Vespertilio noctula	102°.
———Vespertilio pipistrellus	105° to 106°.
Ape.—Simia aigula	103·86°.
Porpoise.—Delphinus phocæna	95·90° to 99·50°.
Narwhal.—Monodon monoceros	96°.
Whale.—Balæna mysticetus	102°.

From this table it appears, that the heat of the body varies in the different genera of mammalia; and it is also seen, that there is no remarkable difference between the cetacea and the other mammalia in respect to their temperature.

The temperature of the body in birds seems, from the following

* Froriep's Notizen, N. 686.

† Tiedemann's Physiologie, i. p. 454.—The English translation, p. 234.

table, which is also taken from Tiedemann, to be, almost without exception, higher than in man and mammalia.

The gull.—Larus has a temperature of	100° Fahr.
White game.—Tetrao albus . .	102°.
Common cock . . .	102·99° to 103·78°.
Common hen . . .	102·99° to 109·94°.
Pigeon . . .	106·70° to 109·58°.
Anas, different species, . . .	106° to 111°.
Bearded vulture.—Vultur barbatus .	107·49°.
Falco, different species, . . .	104·50° to 109·74°.
Raven.—Corvus corax . . .	105·99° to 109·23°.
Fringilla, different species, . .	107° to 111·25°.
Great titmouse.—Parus major . .	111·25°.
Hirundo lagopus . . .	111·25°.

Production of animal heat in old age and early life.—Edwards found the power of generating heat to be less active in old people. It was shown by the experiments of Autenrieth and Schultz,* that the embryo of mammalia owes its heat to the mother, and loses it when removed from the uterus. The same rapid diminution of temperature was observed by M. Edwards in the new-born young of most carnivorous and rodent animals when they were removed from the parent, the temperature of the atmosphere being between 50° and 53½° Fahr.; whereas, while lying close to the body of the mother, their temperature was only 2 or 3 degrees lower than hers. The same law applies to the young of birds. Young sparrows, a week after they are hatched, have, while in the nest, a temperature of 95° to 97°; but, when they are taken from the nest, their temperature falls in one hour to 66½°, the temperature of the atmosphere being at the time 62½°. Other experiments, which M. Edwards instituted, showed that the want of feathers is not the cause of this rapid cooling.† It appears from his investigations, that several kinds of mammiferous animals are born in a much less perfectly developed condition than others; that the young of dogs, cats, and rabbits, for example, are far inferior in the power of generating heat, to the young of other animals which are not born blind. In fourteen days this defect is removed, and they have then reached the stage at which the young of these other animals are born.‡ The need of external warmth to keep up the temperature of new-born children is well known; it is not less necessary, indeed, than to the young of carnivorous and rodent animals. The statistical researches of M. Edwards have shown that the want of external warmth is a much more frequent cause of death in new-born children than has been hitherto supposed. §

* Experimenta circa calorem fœtus et sanguinem. Tub. 1799.

† Froriep's Notizen, 151.—Edwards, On the Influence of Physical Agents on Life, translated by Drs. Hodgkin and Fisher, p. 117—121.

‡ Compare Legallois, Meckel's Archiv. iii. 454.

§ Edwards, loc. citat.

Effects of cold on adult animals.—Hybernation.—The generation of caloric in adult warm-blooded animals is in a certain measure independent of external temperature: this independence, however, varies in degree according to the geographical distribution, and the internal vital conditions of the animal; hence the migrations of many animals with the change of the seasons. But it appears from Captain Parry's observations, that the mammiferous animals of polar regions will support the temperature at which mercury freezes, namely, —40° Fahr., or even a temperature as low as —51° Fahr.* There are some mammalia, however, namely, the hybernating animals—the marmot, rellmouse, hamster, hedgehog, bat, beaver, and bear,—which, when the external temperature is not low, maintain an animal heat which does not differ from that of other mammalia, but lose this heat when the surrounding atmosphere becomes very cold, and fall into a state of torpor or asphyxia, and several of them even become frozen at 10° or 6½° Fahr. The beaver and bear hybernate but imperfectly.

The phenomena of hybernation have been studied more especially by Pallas, Spallanzani, Mangili, Prunelle, and Saissy. As long as the external temperature is as high as 50° or 52½°, the phenomena of hybernation are not induced: the hazel-mouse, indeed, retains, Saissy† says, all its vivacity at 43¼°; Spallanzani had stated the contrary. Saissy also refuted Mangili's assertion, that hybernation is independent of external temperature, and neither commences later nor ceases earlier when the winter is late and the spring early. Pallas induced sleep in marmots during summer by placing them in an ice-house; and Saissy succeeded in the same manner in producing this state in hedgehogs, and rellmice — myoxus glis. In the depth of winter these animals awake, if placed in a temperature of 52¼° or 54½°.

[Berthold‡ has kept dormice—myoxus avellanarius—throughout the winter in a room, the temperature of which was never lower than 50° Fahr., generally was between 59° and 63½°, and sometimes was as high as 70½°, without the animals being roused from their torpid state. He hence concludes that neither external cold nor the necessity of external warmth for the maintenance of internal heat is the cause of hybernation. But that external temperature has a great influence on hybernation is evident from Berthold's own experiments; for the animals which he kept in a warm room were much more easily roused than those which were exposed to the cold of the season: the animals exposed to the cold air fell into the state of hybernation in October; while those which were kept in the room, did not become torpid before the middle of December; and when the torpor of these latter animals was not com-

* See Tiedemann, loc. cit. pp. 461. 466. Translation, p. 236.

† Mém. de Turin, 1810—12. Meckel's Archiv. für Physiol. iii. p. 133.

‡ Müller's Archiv. 1837, p. 67.

plete, it was always rendered deeper by a sudden change from mild to severe weather, and *vice versâ.*]

The temperature of the animals during hybernation, although it falls proportionately with the temperature of the surrounding air, still is $4\frac{1}{2}°$ Fahr. higher than it. Respiration is kept up, though slowly and almost imperceptibly. The marmot during hybernation breathes seven or eight times in a minute, the hedgehog four or five times, the great dormouse nine or ten times in the same period. During the state of the deepest torpor, however, respiration ceases entirely; and the animals may then, if Spallanzani's observation is correct, be placed with impunity in an irrespirable gas. Saissy found that until this last state ensues, they continue to remove the oxygen from the air, the quantity of oxygen consumed decreasing as their temperature falls; but it still continues, together with the exhalation of carbonic acid, as long as any oxygen remains in the air; whereas animals which do not hybernate, such as rabbits, rats, and sparrows, die when they have consumed a small portion only of the oxygen of the air contained in the vessels. M. Prunelle states that the arterial blood of the bat is less bright in colour during hybernation. With respect to the circulation, Saissy found that, at the commencement and towards the termination of the state of hybernation, the motion of the blood is extremely slow; and that while the torpor is complete, the capillaries of the extreme parts are almost empty, and the large vessels only half distended. It was only in the larger trunks of the chest and abdomen that an undulatory motion of the blood was still observable. In the bat during hybernation the heart beats, according to Prunelle, only fifty or fifty-five times in the minute, while ordinarily it beats about two hundred times in the same interval. Sensibility, and the irritability of the muscles, as tested by mechanical or galvanic stimulants, are diminished, but are not entirely wanting, except during the state of the deepest torpor. This entire absence of sensibility and irritability of the muscles has been witnessed by Saissy a few times only in hedgehogs and marmots. The secretions do not wholly cease; for Prunelle found that bats lost $\frac{1}{32}$ of their weight between the 19th of February and the 12th of March.

Saissy states moreover that the blood of the marmot and hedgehog is remarkable for the small quantity of fibrin and albumen which it contains; that the bile is sweetish, but that the fat is unchanged. According to Prunelle and Tiedemann,* an apparently glandular but really fatty mass forms in the neck and anterior mediastinum before hybernation: this fatty mass, Jacobson† remarks, was incorrectly compared with the thymus gland. Otto‡ has discovered a vessel, which might be com-

* Meckel's Archiv. t. i. p. 481.

† Ibid. iii. 151, 152.

‡ N. act. ac. cæs. nat. cur. t. xiii. p. 1.

pared to the internal carotid, passing through the stapes of the tympanum in the following genera, Vespertilio, Erinaceus, Sorex, Talpa, Hypudæus, Georhychus (Lemmus), Myoxus, Mus, Cricetus, Dipus, Meriones, Arctomys, and Sciurus; all of which animals, Otto says, are subject to a state of more or less complete hybernation. The assertion of Mangili, that the cerebral vessels are remarkably small in hybernating animals, is denied most expressly by Otto, who also did not observe the large size of the nerves of the superficial parts, which was spoken of by Saissy. It is generally known that, during hybernation, a part of the fat formed in the autumn is consumed to nourish the body. But the experiments of Pallas, who produced hybernation during the height of summer by means of artificial cold, prove the incorrectness of the theory, which supposes that it is the accumulation of fat, and the enlargement of the glands in the chest and neck during the autumn, which induce hybernation, by exerting pressure upon the respiratory nerves. The spinal cord is very short in the hedgehog; but this is not a general character of hybernating animals.*

Effects of external heat on the temperature of warm-blooded animals.—If the temperature of the atmosphere, in which a mammiferous animal is placed, exceeds the natural heat of its body, a slight elevation takes place in the temperature of the animal's body, not however in proportion to the elevation of the external temperature. Experiments have been instituted by Duntze,† Fordyce, Banks, Blagden,‡ and Delaroche, and Berger, to ascertain the effect of increased external heat on the temperature of the body. Sir C. Blagden and others supported a temperature between 198° and 211° Fahr. in a dry air for several minutes; [in a subsequent experiment Blagden himself remained eight minutes in a temperature of 260°;] Delaroche and Berger observed an elevation of temperature of a few degrees only in rabbits exposed to a heat varying from 122° to 194° Fahr. In birds also the heat of the body did not rise commensurately with that of the surrounding atmosphere: it did not suffer an elevation of more than 11 or 12 degrees.§ This power of maintaining nearly their original temperature when exposed to great external heat, is owing to the cooling effect of the in-

* The principal treatises on hybernation are:—Saissy, Recherches experimentales anatomiques sur la physique des animaux mammifères hybernans; Paris et Lyon, 1808; übersetzt von Nasse. Reil's Archiv. für Physiol. t. xii. p. 293. Saissy, Mém. de Turin, 1810—1812. Meckel's Archiv. für Physiol. t. iii. Mangili über den Winterschlaf, in Reil's Archiv. Bd. 8. Prunelle, Recherches sur les phénomènes et sur les causes du sommeil hivernal: Ann. du Mus. t. xviii. Gilbert's Annalen, Bd. 40 u. 41.

† Exp. calorem animalium spectantia. Lugd. Bat. 1754.

‡ Philos. Transact. 1775, v. 65.

§ Delaroche and Berger, Exp. sur les effects qu'une forte chaleur produit dans l'économie animale. Paris, 1806. Journal d. Phys. 71. Reil's Archiv. 12. 370.

creased perspirations which animals suffer under these circumstances. The correctness of this explanation is proved by the circumstance observed by Delaroche, that if the heated atmosphere is at the same time saturated with moisture which prevents exhalation taking place, the temperature of the animals rises 4, 7, even 9 degrees higher than that of the surrounding atmosphere. It must not, however, be forgotten that the increased evaporation from the surface of the body in a dry heat does not arise solely from physical causes, but that the external heat here excites an organic function. In fact, when there is great internal heat, evaporation is often prevented by internal causes; and in many fevers the skin is intolerably hot, merely from its being dry, and from perspiration being obstructed.

Temperature of cold-blooded vertebrata.—It has been often said, but incorrectly, that cold-blooded animals have themselves no power of generating heat, but derive their temperature solely from the surrounding medium. With respect to the reptiles and amphibia, the researches of Dr. Davy, Czermack, Wilford, and Tiedemann, have proved that the temperature of these animals, although it generally falls with that of the surrounding medium to a certain point, is nevertheless mostly two or more degrees higher; and that although their temperature rises also with that of the medium, yet at a certain point it ceases to be higher, and at great degrees of heat is even lower than the external temperature. From Czermack's* experiments, it appears that in amphibia the temperature of the body exceeds that of the medium less than in reptiles. Thus the temperature of the body of a proteus was $63\frac{1}{2}°$ Fahr. when that of the air was $55\frac{1}{2}°$,—was $68\frac{1}{4}°$ when the temperature of the air was $63\frac{1}{2}°$,—and was 65° in water of a temperature of 55°. In water, of which the temperature was $44\frac{1}{3}°$, the temperature of a frog was 48°; in air of $54\frac{3}{4}°$, was $46\frac{1}{4}°$. Czermack found that of reptiles, lizards and serpents are those in which the temperature of the body differs most from that of the atmosphere, to the extent, namely, of several degrees. Dr. Davy † also found the temperature of a snake 88·46° in air of 81·50° Fahr., and 89·99° in air of 82·94°; while the temperature of a testudo mydas was only 84°, the heat of the atmosphere being 85·13°, and only 85° when the heat of the atmosphere was 86°.

Tiedemann‡ observed, that at night, when the water was frozen, a frog had a temperature of 33° Fahr., and the water around it was unfrozen. Frogs seem also to have the power of preserving a low temperature in a great external heat by means of exhalation. Fishes also, it appears from the experiments of Martine, J. Hunter, Broussonet, and

* See the numerous experiments of Czermack on the temperature of reptiles in Baumgaertner's and Ettinghausen's Zeitschrift für Physik und Mathematik, 3 Bd. 385. † Froriep's Notiz. 579. Philos. Trans. 1814. Jameson's Journal, v. xix.

‡ Tiedemann, Physiol. i. Translation by Drs. Gully and Lane, p. 240.

Dr. Davy, have a temperature one or two degrees higher than that of the surrounding water. In small fishes Broussonet found the difference of temperature between their bodies and the water to be from $\frac{9}{10}$ of a degree to $1\frac{1}{5}°$ Fahr.; in the eel $1\frac{1}{3}°$; in the carp $1\frac{4}{5}°$. Despretz found the temperature of two carp to be 53° Fahr., of two tench $52\frac{3}{4}°$ Fahr.; the temperature of the surrounding water being $51\frac{1}{2}°$ Fahr. Dr. Davy ascertained that the temperature of a shark was 77° Fahr. when the temperature of the sea was $42\frac{3}{4}°$ Fahr.

[Some new and careful experiments on the temperature of cold-blooded animals have been instituted by Berthold.* He finds that the absence or existence of a great difference between the temperature of these animals, and that of the medium, depends wholly on the circumstance of the temperature of the medium having been stationary for some time, or having recently become elevated or lowered; for, if the temperature of the medium has changed, a considerable time is required for the heat of their bodies to undergo a corresponding change. Avoiding this source of error, Berthold found that amphibia had generally a lower temperature than the surrounding air, which arose from the cooling effect of evaporation. In water, frogs had the same temperature as the water. During the act of copulation, the frogs had a temperature $\frac{1}{4}°$ to 1° R. or $\frac{1}{2}°$ to $1\frac{4}{5}°$ Fahr. higher than that of the water. Reptiles, when the external temperature is moderate or rather elevated, have a heat $\frac{1}{2}°$ to $1\frac{4}{5}°$ Fahr. higher than air or water exposed to the same atmosphere.]

Some cold-blooded animals also present the phenomenon of hybernation. Franklin relates, that many fishes, when laid upon the ice, became instantly torpid, but recovered again after several hours or days. It has, however, been frequently asserted, that fishes continue to live in ice, and that the water around them is not frozen.† Pallas‡ relates, that crucians (cyprinus carassius) are restored to life on the melting of lakes in Siberia, which were frozen to the bottom, and mentions a similar fact observed by Bell, namely the revival of gold-fishes from frozen water. Reptiles become torpid not only during winter, at the commencement of which they bury themselves, but during summer also, in hot climates. In the dry season reptiles bury themselves and fall into a state similar to hybernation, from which they recover in the rainy season. Humboldt has observed some very interesting facts of this kind. In warm-blooded animals there is only one known instance of this summer sleep; that is in the tanrec,—the hedgehog of Madagascar.

Temperature of invertebrate animals.—Some complete observations on the temperature of invertebrate animals are still wanted, but the facts

* Neue Versuche über die Temperatur der Kaltblütigen Thiere. Götting, 1835. Müller's Archiv. 1836, Jahresbericht, p. cxix.

† Jahresbericht der Schwed. Acad. übersetzt von J. Müller, 1824.

‡ In Rudolphi's Grundriss der Physiologie, i. p. 176.

that are known prove that their temperature, like that of the other cold-blooded animals, varies with the temperature of the medium; but that it may nevertheless, even in insects, be a degree or two higher or lower than the external temperature is evident from the experiments of Martine, Hausmann, Rengger, and Dr. J. Davy; while in bee-hives and ant-hills a very much higher temperature has been observed.* In the river crawfish, Rudolphi saw the thermometer, which in the water was at $52\frac{1}{4}°$, rise to $54\frac{1}{2}°$, and even to 59° F. Similar evidences of independent heat, though less considerable, have been observed in the mollusca.† In snails the temperature is two degrees higher than that of the medium.

The insects and mollusca, of temperate and cold climates at least, are known, with certainty, to be subject to hybernation. Some of the lower animals seem to require a pretty high external temperature. The instance of the small snail,—the cyclostomum thermale Ranzani,—which lives in the hot springs of Abano, the temperature of which is $83\frac{3}{4}°$ F. appears extraordinary. Rudolphi saw these animals move briskly even in water of $99\frac{1}{2}°$ F. But the entozoa of man and mammalia live in an equal, those of birds in a still higher temperature. Rudolphi remarks, that the entozoa of warm-blooded animals become torpid in the cold, but are again revived when placed in warm water; while the entozoa of cold-blooded animals bear a low as well as a high temperature.

The hybernation of snails has been described by Gaspard; during this state the heart, he says, ceases to beat, respiration is no longer carried on, and the tentacula, if cut off, are not reproduced. These animals also fall into a summer sleep when the heat is great; but, in the summer sleep, respiration, the heart's action, and the reproductive power are not interrupted.‡

Sources of animal heat.—I now proceed to inquire what are the processes by which heat is generated in the animal body. The first point of interest in this inquiry is the difference of temperature of different parts of the body. The temperature is lower, the further removed the part is from the centre of the body; thus, in the human subject, a thermometer placed in the axilla stood at 98° F. at the loins it indicated a temperature of $96\frac{1}{2}°$, on the thigh 94°, on the leg 93° or 91°, on the sole of the foot 90°.§ Dr. J. Davy found the temperature of the rectum, in several experiments, somewhat higher than that of the brain; this appears extraordinary, and probably arose from some error of observation. Dr. Davy's experiments on the temperature of the different kinds of blood are very interesting. Eleven experiments were instituted on sheep

* See note at end of Prolegomena.

† An account of the different observations relative to this subject will be found in Rudolphi's Physiolog. 179, in Treviranus, Biologie, 5—20, and in Tiedemann's Physiol. 476; Translation, p. 244.

‡ Meckel's Archiv. 8.

§ Dr. J. Davy, Phil. Transact. 1814. Meckel's Archiv. ii. p. 312.

and oxen; and from the mean of these experiments it would appear that the temperature of arterial blood is about 1° or $1\frac{1}{2}$° F. higher than that of venous blood.* Mayer† found the temperature of the blood of the jugular vein to be from 1° to 2° R. or from $2\frac{1}{4}$° to $4\frac{1}{2}$° F. lower than that of the blood of the carotid; but he could not discover the difference of temperature of the blood of the two sides of the heart, which is spoken of by Davy. Saissy has made similar observations in hybernating animals.

Theory of the production of heat in respiration.—According to the theory of respiration, invented by Lavoisier and Laplace, and adopted by most modern chemists, the oxygen of the atmosphere combines in the lungs with carbon of the blood, and is expired in the form of carbonic acid; and if more oxygen disappears from the atmosphere than is accounted for by the carbonic acid expired, it is supposed that this portion of the oxygen which does not go to form carbonic acid, unites with hydrogen in the blood and forms water, which is exhaled. Admitting these hypotheses, it might be imagined that the source of animal heat was the caloric developed during the combination of the oxygen with the carbon and hydrogen in the lungs. To render this more probable, and to explain more easily the distribution of the caloric, when developed, through the body, Dr. Crawford ‡ stated, that arterial blood has a greater capacity for caloric than venous blood, about in the proportion of 11·5 to 10. Thus he supposed, that the caloric developed in the lungs at first served to maintain the temperature of the arterial blood, and that afterwards, during the conversion of this arterial blood into venous blood in all parts of the body, the heat, before latent in the arterial blood, was set free. Dr. J. Davy has, however, shown, that the capacity of the two kinds of blood for caloric differs, either not at all, or only very slightly, as in the proportion of 10 to 10·11.

But, supposing that Lavoisier's theory of respiration is correct, the amount of caloric that can be generated by the respiratory process may be ascertained by direct calculation. This calculation has been made by Dulong and Despretz. Dulong introduced different mammiferous animals, carnivorous as well as herbivorous, into a receiver, in which the changes produced in the air by respiration, and the volume of the different products, could be determined, at the same time that the amount of caloric lost by the animal could be ascertained. Dulong found, that all animals extracted from the air more oxygen than was accounted for by the carbonic acid which they exhaled. In herbivorous animals, the oxygen thus lost amounted on an average only to $\frac{1}{10}$ of the whole quantity of

* Davy. Tentamen experimentale de sanguine. Edinb. 1814. Meckel's Archiv. i. 109. Phil. Transact. 1814.

† Meckel's Archiv. iii. 337.

‡ Dr. Crawford, on Animal heat. Versuche und Beobachtungen über die Wärme der Thiere. Leipzic, 1799.

the oxygen extracted from the air; in carnivorous animals, the maximum quantity of this oxygen, which was not converted into carbonic acid, was $\frac{1}{2}$, the minimum $\frac{1}{5}$, of the whole amount of oxygen consumed. If now it be admitted, that, by the conversion of the oxygen into carbonic acid during respiration the same quantity of caloric is developed as Laplace and Lavoisier found to be produced by the combustion of carbon in oxygen gas, it will be found by calculation that only $\frac{7}{10}$ of the heat that is lost during a given time by herbivorous animals, and $\frac{1}{2}$ of that which carnivorous animals lose in the same space of time, can be thus accounted for. Again, admitting that the oxygen, which is converted intocarbo nic acid, is consumed in forming water by uniting with hydrogen, and that as much caloric is thus generated as would be developed during the combustion of equal quantities of oxygen and hydrogen, still the whole quantity of caloric produced by the combination of carbon and hydrogen with the oxygen, would amount only to from $\frac{3}{4}$ to $\frac{4}{5}$ of that which is developed during the same space of time by carnivorous as well as herbivorous animals.*

Despretz placed animals in a vessel surrounded with water; an uninterrupted current of air to and from the vessel was maintained, and the volume and composition of the air both before and after the experiment, which was continued $1\frac{1}{2}$ or 2 hours, as well as the increase in the temperature of the surrounding water, were ascertained: by this means he found that the heat, which would have been generated in the respiratory process according to Lavoisier's theory, would have accounted for from 0·76 to 0·91 of that which the animals really gave out during the same time.†

From these experiments it results, that, even if the chemical theory of respiration is adopted, there must be still some other source of animal heat. But it is exceedingly improbable that the water exhaled from the lungs is formed during the respiratory process by the union of its elements; it is much more probable that a part of the oxygen is retained by the blood: the heat produced by the process of respiration, therefore, can be estimated as being derived only from the union of the oxygen and carbon, and the heat thus generated would, according to Dulong, amount in herbivora to $\frac{7}{10}$ only, and in carnivora to $\frac{1}{2}$ only of the heat really developed in the body. Besides, it is at present merely an hypothesis that the oxygen of the atmosphere unites with the carbon in the lungs to form carbonic acid; although new facts render it exceedingly improbable, that the carbonic acid exists already formed in the venous blood, and is merely exhaled in the lungs, while the oxygen combines with the blood. According to this latter view, which would

* Berzelius, im Schwedischen Jahresbericht; Boun, 1824, p. 67. See also Neues Journal für Chemie und Physik. N. R. Bd. 8. S. 505.

† Gmelin's Chemie, t. iv. p. 1523. Ann. d. Chim. et de Phys. 26, 338.

explain the phenomena equally well, the oxygen combines with the carbon in the course of the circulation, and thus imparts to the blood a higher temperature. Wherever the carbonic acid is formed,—whether in the lungs or in the blood,—the oxygen inspired would in either case be the immediate source of its formation, and respiration might be regarded as the cause, mediate or immediate, of the developement of animal heat; and, adopting the results obtained by Dulong, it might be admitted that in herbivora $\frac{7}{10}$, in carnivora $\frac{1}{2}$, of the animal heat is generated by respiration. This being conceded, it would be easy to explain the want of perceptible independent heat in the embryo, in which no oxygen is inspired; and the circumstance that the subjects of the morbus cœruleus, (in which respiration is impeded from defect of the circulatory organs), have sometimes a temperature some degrees lower than natural, as well as the small degree of independent heat possessed by cold-blooded animals, (in which only a part of the blood is aerated, as in reptiles, or in which respiration is performed only by means of the air dissolved in water, and is consequently less perfect,) might then be likewise easily accounted for. To put the chemical theory of animal heat to a decided test, experiments must be instituted on the plan of those of Dulong and Despretz, but on cold-blooded in place of warm-blooded animals, to ascertain whether, calculating from the changes produced in the air by respiration, the quantity of caloric generated by the chemical process would not be too large, compared with the very small quantity of heat really evolved by the former animals. This is an interesting problem for chemical inquiry.

Generation of heat in the organic processes.—There must be other sources of animal heat, besides respiration. Some physiologists, and among them Professor von Walther and Dr. Paris, have thought to find a principal source of animal heat in the different secreting processes, in which fluids having a less capacity for caloric than the blood are separated from the latter fluid, and caloric before latent thereby rendered sensible. According to Dr. Crawford, the capacity of milk for caloric is less than that of the blood. Dr. Paris* estimates the capacity of urine for caloric at 0·777, that of arterial blood at 1·003. These results are directly opposed to those obtained by Dr. Nasse, who found no difference, as regards their capacity for caloric, between the different secretions and water; and Dr. Davy detected scarcely any difference in this respect between the blood and water. M. Pouillet† has directed attention to another source of heat in the vital processes. All solid bodies, inorganic as well as organic, undergo an elevation of temperature when moistened with different fluids. This elevation of temperature is much greater in organic substances; in several cases M. Pouillet found that it amounted to from 11° to 18° of Fahrenheit.

* London Med. and Physic. Journal. 21. 1809. Meckel's Archiv. ii. 308.

† Ann. Chem. Phys. 20, 141. Meckel's Archiv. viii. 233.

The solution of the food by the fluids of the stomach might be taken as an example, and perhaps the slight increase of heat during digestion might be thus explained. But a more considerable and more general source of animal heat is undoubtedly to be sought in the organic processes, in which by the operation of the organising forces on the organic matter heat is generated not in one, but in every organ of the body: hence it is, that in cases of long fasting, in which the separation of the old matter continues, but not the organisation of new matter, the temperature of the body, according to Martine, falls considerably, to the extent even of several degrees, although at the same time the source of caloric in the formation of carbonic acid remains. In inflammation the flow of blood to the part is increased, and the temperature is at the same time elevated; but Dr. J. Thomson* thinks that it never rises higher than the temperature of the blood in the great vessels. Muscular exertion and febrile irritation also cause elevation of temperature; while the depression of vital energy in nervous affections, and in rigors, causes the temperature of the body to fall, although respiration is unaffected. Dr. Currie† found the temperature in the palm of the hand during syncope to be as low as 63° F.

Influence of the nerves in the generation of heat.—Now, since all organic processes are chiefly dependent on the influence exerted by the nerves on the organic matter of the body, it cannot appear wonderful if the reciprocal action between the organs and the nerves is a main source of animal heat. The experiments of Brodie, Chaussat, and others, have proved this. Elliot and Home have observed, that, after division of the nerves of a limb, its temperature falls, and all observers confirm this result in the case of the nervus vagus. The diminution of temperature is detectible by a thermometer; the mere sensation of cold after injury to the nerves of a limb must not be confounded with it. Mr. Earle‡ found the temperature of the hand of a paralysed arm to be 70° Fahr., while that of the sound side had a temperature of 92° Fahr. On electrifying the limb, the temperature rose to 77°. In another case the temperature of the paralysed finger was 56° Fahr. while that of the unaffected hand was 62°.

Brodie§ having killed an animal, either by decapitating it, by dividing its medulla oblongata, by destroying its brain, or by poisoning it with Worara poison, kept up artificial respiration, and found that the action of the heart continued, and that the blood became arterialised in the lungs

* Lectures on Inflammation. Edinb. 1813, p. 46.

† Currie, Wirkungen des Kalten und Warmen Wassers. Leipzic, Bd. i. p. 267. Currie on Cold Affusion.

‡ Earle, in Med. Chirurg. Transact. vii. p. 173. Meckel's Archiv. iii. p. 419. See also Yelloly in Med. Chir. Transact. iii.

§ Sir B. Brodie, in Phil. Trans. 1811, 4; 1812, 378. Reil's Archiv. 12, 137, 199.

as during life, but that the heat of the body was not maintained; indeed, it became cold more rapidly than a body in which artificial respiration was not kept up, being cooled by the air forced into the lungs. Dr. Marshall Hall,* however, observed the very contrary of this; he found that a decapitated animal retained its warmth longer, when artificial respiration was performed. The results obtained by Legallois,† also, do not exactly agree with those of Brodie's experiments; Legallois found that every impediment to respiration, whether from the animal being fixed upon its back, or from the air which it breathes being rarefied or mixed with nitrogen or carbonic acid, is attended with a diminution of temperature; that even the inflation of the lungs with air, by impeding the process of respiration, causes diminution of the heat of the body, and that the greatest degree of cold always corresponds to the smallest consumption of oxygen. Emmert‡ repeated Brodie's experiments with poison and artificial respiration, and found a change of temperature of only $6\frac{3}{4}$° Fahr. in the space of 74 minutes. Wilson Philip§ infers from his own experiments, that artificial respiration, when the inflation of the lungs is performed too frequently, cools the body very quickly, but that when employed with moderate frequency it retards the cooling of the body. Brodie's experiments are, however, for the main point, convincing. He has shown, that living rabbits expire 28·22 cubic inches of carbonic acid in half an hour; that, when artificial respiration is kept up in rabbits after death by poisoning, or destruction of the medulla oblongata, a quantity of carbonic acid, varying from 20·24, or 25·55, to 28·27 cubic inches, is still exhaled; thus, that under these circumstances, the products of respiration are nearly the same as ordinarily during life, and that, nevertheless, the temperature falls six degrees of Fahrenheit in the course of an hour.‖ The sinking of the temperature of the body, which Legallois stated to be constant in animals fastened down upon their back, was not observed by Chaussat ¶ in dogs; on the contrary, Chaussat confirms Brodie's observations. After injury of the brain, the temperature fell from 104° Fahr. to 75° before death, which occurred in from eleven to twenty-two hours. Division of the nervous vagus, which, without essentially affecting the chemical process of respiration, produces death, according to Legallois, by inducing congestion of the lungs with serum or blood, caused the temperature of the body to fall, during a period

* London Med. Phys. Journal, 32, 1814. See also Brodie, ibid. p. 295. Meckel's Archiv. iii. 429, 434.

† Ann. Chem. Phys. 4, 1817. Meckel's Archiv. iii. 436.

‡ Meckel's Archiv. 1, 184.

§ Untersuchung. über die Gesetz. d. Function. des Lebens übersetzt. von Sontheimers. Stuttgardt, 1822. Inquiry into the laws of the vital functions.

‖ See Nasse's Remarks on Brodie's experiments in Reil's Archiv. xii. p. 404.

¶ Meckel's Archiv. vii. 282.

varying between twelve and thirty-six hours, as low as 97° or 98½° Fahr. and at last even to 68°. In all these experiments, unfortunately, the temperature of the atmospheric air is not mentioned. Injuries of the spinal marrow produced more striking effects on the animal heat, the higher the seat of the injury; so that the effects on the generation of caloric, like other consequences of lesions of the spinal cord, were greater in proportion to the number of nerves arising below the point of injury.

Chaussat endeavours lastly to prove, that the sympathetic nerve also has a great share in the production of animal heat: he found, that after injury of the splanchnic nerve, produced in the extirpation of the supra-renal capsule through a wound, which, he says, was not very large, (?) the temperature gradually fell from 104·88° to 78·8° Fahr. during the ten hours which preceded death. Chaussat applied a ligature to the aorta of a dog, at the point where it passes through the aortic opening of the diaphragm, and then examined the temperature of the upper and lower half of the animal; he repeated this experiment, and each time it appeared that the œsophagus, up to the time of death, had a somewhat lower temperature than the rectum. This slight difference is attributed by Chaussat to the cooling effect of respiration. Chaussat thence inferred that much less influence on the developement of animal heat is exerted in the thorax than in the abdomen through the medium of the nerves. The diminution of temperature, which ensues on division of the nervus vagus, cannot be assumed to prove the contrary, for this nerve supplies branches to abdominal as well as to thoracic organs. But Chaussat here attributes great importance to indecisive experiments, which prove little or nothing, and does not perceive how many objections might be made to them.

Several of the facts which we have mentioned prove, however, that the influence of the nerves in the organic processes of the body contributes greatly to the production of animal heat in other parts than the lungs. Berzelius is also of this opinion, which moreover seems to derive confirmation from the rapid and momentary increase of temperature, sometimes general, at other times quite local, which is observed in states of nervous excitement; from the general increase of warmth of the body, sometimes amounting to perspiration, which is excited by passions of the mind; from the sudden rush of heat to the face, which is not a mere sensation; and from the equally rapid diminution of temperature in the depressing passions;—all phenomena, however, which might certainly be explained by the increased or diminished flow of blood to the part, and in some cases also by a change induced in the heart's action. From the facts at present known, the inference we deduce is, that elevation of temperature takes place in all organic processes, but that it is in part determined by the influence exerted on these processes by the nerves.

[MM. Becquerel and Breschet* have observed that each contraction of a muscle is attended with an elevation of its temperature, amounting to 1°—2° cent. or $1\frac{4}{5}$°—$2\frac{3}{5}$° Fahr. They ascertained the temperature of any part by means of thermo-electric multiplier, a needle composed of two other needles united at their point being thrust into the part, while the other extremities of the needles were connected with the wires of the multiplier.]

If now the warm-blooded and cold-blooded animals are compared, the cause of the difference of temperature in the two may be sought, either in the relative intensity of the respiratory process, or of the organic processes generally. Without referring one phenomenon to another as its cause, it may be remembered, that in the cold-blooded animals the size of the central portions of the nervous system is smaller in proportion to the nerves themselves; that the respiratory process is far less active in proportion to the weight of the body; that the blood of these cold-blooded animals contains, according to Prevost and Dumas, less coagulable matter; a similar state of the blood being also found by Saissy in hybernating animals; and, lastly, that birds and some mammalia, the blood of which, according to Prevost and Dumas, contains a larger quantity of red particles and coagulable matter, also have a higher temperature.

Cause of hybernation.—Before all these facts with respect to the cause of animal heat were considered, no inquiry with reference to the spontaneous diminution of this power of generating heat during hybernation, and regarding the causes of this latter phenomenon, could be attended with any satisfactory result. In this inquiry the phenomenon of hybernation as presented by a few animals must not be considered in an isolated manner, but the investigation must be grounded upon the fact, that all animals, when the external temperature falls below a certain point, become torpid and frozen, without thereby entirely losing the faculty of living; but that the point to which the external temperature may be lowered without this state being induced, varies very much according to the organisation of the different animals, and their geographical distribution.

1. Man evidences in this respect a very great tenacity of the organic powers, since he maintains his proper temperature, under favourable circumstances, in all climates in which animals exist,—in the extreme north, as well as under the equator. But even man, when deprived of necessary covering and acted on by cold, or, in other words, deprived of a vital stimulus, falls into a state of torpor, and the more easily when his vital force is depressed by the influence of intoxicating substances.

2. Many animals fall readily into this state of torpor, when the neces-

* Ann. d. Sc. Nat.—Mai. Oct. Müller's Archiv. 1836. Jahresbericht, p. cxix.

sary degree of external warmth which determines their geographical distribution is wanting; it is from the necessity of a certain external temperature that birds migrate.

3. The young of mammalia become torpid at a temperature which is sufficiently elevated for maintaining the vital force of the adult animals in an active state. This is proved by the observations of Legallois, on rabbits six or eight weeks old, which however may be restored from the torpid state by raising the temperature of the medium.

Now, the cold in these cases does not exert a direct depressing effect on the respiratory process: all the first symptoms of the torpor from the influence of cold, namely, the insensibility, sleepiness, and debility, are rather indicative of depression of vital force from want of vital stimulus; the subsequent effect on the respiration must therefore be regarded as a consequence, not as the cause of this torpor, just as in the case of syncope from nervous affections; and the diminution of the temperature of the body is likewise a consequence of the depression of vital energy, which might perhaps prevent the generation of caloric supposed to take place in the lungs, by primarily causing retardation of the respiratory movements, and rendering the respiratory process less active. The facility with which this state of torpor is induced in some animals arises therefore from the greater delicacy of their structure, and from the vivifying and stimulating influence of warmth being more necessary for the continuance of their organic processes. This must also be regarded as the cause of the winter sleep of hybernating animals, in which the only great peculiarity is, that in them the torpor may continue a long time without danger to life. Of the causes of hybernation advanced by Saissy and others, some are merely consequences of the depression of the vital energy; others, such as the supposed large size of the external nerves and small size of the cerebral vessels, do not exist.

The *hybernation* of animals then is perfectly analogous to what is called the nocturnal sleep of plants,—the change of position of their leaves,—which is also occasioned by want of external stimulus, namely, the light; and is sometimes observed during the day, when plants are in the shade.* The ordinary sleep of animals, on the contrary, is by no means dependent on want of stimulus, but arises from the material change and exhaustion induced in the body by the state of action, and may, therefore, occur naturally at any time of the day, although from accidental causes it mostly comes on at night.

The *summer sleep* of reptiles and of the tanrec seems, on the other hand, to arise from a disturbance of the system induced by too much heat. The want of water also appears to be a main cause of this state, which

* Journ. de Phys. 52. 124.

may therefore be regarded as the effect of the want of one vital stimulus, and of the excess of another.*

These facts relative to winter and summer sleep, are closely connected with the known depressing effects of a long-continued high temperature on the functions of the nervous system in man, and this is a very fit occasion for comparing the effects of heat and cold. Both may induce a disturbance of the excitability of the body, as well as irritation, inflammation, and sphacelus. The sudden violent action of cold on warm animal tissues has a disorganising effect. Very cold bodies, when touched, produce a sensation of pain and then numbness. When the cold is more extreme, sphacelus or local death ensues. A slighter application of cold, by extracting the animal heat, produces symptoms of inflammation and irritation, from the effort which is made by nature to restore the balance in the part. A moderate degree of cold has at first an exciting effect. Thus cold water produces instantaneous reddening of the skin, as I have myself observed when bathing in the month of October; but this effect is only momentary, and the phenomena of disturbance of the internal organs from extraction of heat soon follow. Cold is sometimes used in this way, as a stimulant, to produce a temporary disturbance of the nervous system, which may be beneficial. In fevers with a hot dry skin, cold water often acts indirectly as a vivifying stimulant, and restores the action of the skin, as warmth does in parts suffering from cold. The secondary effects of continued cold are always relaxation of the nervous system. The gradual action of cold to a high degree induces in the human subject a state of torpor, and in hybernating animals the state of hybernation by the withdrawal of a stimulus; while a too elevated temperature also depresses gradually the action of the nervous system, but probably by producing a change of composition; and in the sandy deserts excessive heat with want of water, causes asphyxia, and gives rise to the summer sleep of reptiles and the tanrec in hot climates.

3. *Of the developement of Light in Animals.*

It is now known with certainty that the *phosphorescence of the sea*,—the light visible in the waves, especially in the track of sailing vessels,—which has been observed as far south as 60° S. L. arises from the presence of luminous animals in the water. These animals are in part infusoria, in part polypifera,—veretillum, pennatula,—in which it is chiefly the polypes themselves which are luminous; while many medusæ also, perhaps all those of tropical climates, and some annelides—nereides and polynoe fulgurans,†—planariæ, and mollusca—particularly pholades, salpæ, and

* See also Pastré, Nov. Act. Acad. Nat. Cur. 14. 661.

† For an account of the Polynoe fulgurans, an annelide which contributes to the phosphorescence of the Baltic, consult Ehrenberg in Poggendorf's Annal. d. Physik, 1831, 9.

pyrosomata,—contribute to the phosphorescence of the sea. It appears, that even the water which flows from these animals is also luminous, and that the phosphorescence continues for a certain time after death. When pholades are placed in a vacuum, the light disappears, but becomes again visible on the re-admission of air. When dried, they recover their luminous property in some degree on being rubbed or moistened. Meyen* distinguishes three sources of phosphorescence in the sea: 1. mucus dissolved in the sea-water; 2. animals covered with a luminous mucus, — medusæ, pholades; 3. animals possessing phosphorescent organs, — pyrosoma, oniscus fulgens. In the carcinium opalinum, or oniscus fulgens, special organs for the developement of the light are seated in the fourth and fifth rings of the body. Many other crustacea also seem to be luminous. [Ehrenberg ‡ has discovered that in many medusæ of the Baltic light issues solely from particular parts of the body: in some, as the cydippe pileus and oceania pileata, from the spot where the two ovaries are situated; in others, as the oceania hemispherica, from the base of the cirrhi, or from organs near the cirrhi, and alternating with them at the border of the animal. The dead animals were not luminous in the slightest degree. M. Ehrenberg believes the developement of light to be connected with the sexual function.]

The *luminous insects* are the elater noctilucus, phosphoreus, and ignitus; the pausus sphærocerus, scarabæus phosphoreus, several species of lampyris, and the scolopendra electrica.‡ In the elater, the principal sources of the light are two oval spots at the side of the thorax covered with transparent laminæ. Treviranus could discover no difference between the luminous substance and the fat of the body. In the glowworms, — lampyris noctiluca and splendidula, — the light issues from the under surface of the last three abdominal rings, particularly from two whitish spots on the last ring; the ova of the lampyris splendidula are also luminous, and it seems that the pupa and larva are not entirely without light. In these animals the internal parts of generation, according to Treviranus, are the source of the light. The apparently voluntary influence which the animal exerts over the emission of light, is effected, Treviranus says, by the inspiration of air. All observers except Macartney and Murray agree that in irrespirable gases, and in a vacuum, the phosphorescence ceases, or at least diminishes. After the death of the animal, the phosphorescent property is not entirely extinguished. The luminous parts, even after being dried, recover their brilliancy when moistened with water. The brilliancy of the luminous beetles does not diminish for several hours when they are placed in water, but ceases immediately in oil; it is restored, however, when the

* Nov. Act. Nat. Cur. vol. xvi. suppl.

† Abh. d. K. Academie d. Wissensch. zu Berlin, p. 411. ‡ Trevianus, Biol. 5. 97.

insect, whether dead or living, is exposed to the vapour of fuming nitric acid.* From all the above facts, the opinion of Treviranus appears most probable, namely, that the light is derived from a matter containing phosphorus, which is formed under the influence of light, but, once formed, is in some measure independent of light. Several phenomena would lead us to believe, that the luminous insects absorb light during the day, like the Bononian stones, and emit it in the evening; this was indeed the opinion of Carradori, Beccaria, and Monti, and is supported more especially by the circumstance that this absorption of light is evidenced by several mineral substances such as sulphate of barytes mixed with sulphuret of barium, oystershell heated to redness with sulphur, &c. and also by several organic substances, when dried, such as seeds, flour, starch, acacia gum, quills, cheese, yolk of egg, muscle, tendon, isinglass, glue, and horn. But this opinion does not agree with the observation of Todd and Murray, namely, that glow-worms shine in the evening, even when they have been kept in the dark during the day; Macaire and Macartney, however, deny that this is the case.†

Developement of light in the higher animals.—There is no instance known of the developement of light in any of the higher animals, except, perhaps, the phosphorescence of the ova of lizards, and that which has been sometimes observed in the urine. [Some fishes have been recently discovered to be luminous.‡] The supposed luminous property of the eyes of many mammalia, particularly of the predacious animals, and more especially cats, and also of the eyes of oxen and horses, is now scarcely regarded but as one of the superstitions of medicine. The luminous appearance of the eyes of some animals arises from the reflection of the light from a brilliant tapetum which is devoid of black pigment; for which reason the eye of the white rabbit is especially brilliant, and the eyes of the Albino Sachs are said to have been luminous. Prevost§ was the first to explain the phenomenon; he showed that it could never be seen in complete darkness, and is dependent neither on the will, nor on the passions, but is the effect of the reflection of light which enters the eye from without. Independently of Prevost, Gruithuisen ‖ had observed the same facts. Rudolphi¶ was of the same opinion, and remarks that the appearance of light can be seen only in certain positions, and is also perceptible in the eyes of dead cats, when regarded in a favourable direction**. The Albinos are themselves never sensible of the light which is visible

* On this subject, consult Treviranus, Biologie, loc. cit. Tiedemann's Physiol. i. 488—510. The translation, p. 257—271. Gmelin's Chemie, 81—86.

† Tiedemann's Physiol. i. 503.

‡ Paper by Mr. Bennet, read at the Zoological Society, May 30th 1837.

§ Biblioth. Britannique, 1810, t. xlv.

‖ Beiträge zur Physiognosie und Eautognosie, p. 199.

¶ Physiol. i. 197.

** I have myself made the same remarks. See my treatise "Zur vergleichende Physiologie des Gesichtsinnes;" Leipz. 1826, p. 49.

to others in their eyes.* Esser,† moreover, has shown that the eyes of cats, dogs, rabbits, sheep and horses, are not luminous when external light is perfectly excluded; and that the reflection of light remained the same when the cornea, iris, and lens were removed. I am glad to find Tiedemann's‡ experience correspondent to these observations. He observed the luminous appearance of the eyes of a cat, in a head which had been twenty hours separated from the body. It is then the more astonishing to find the emission of light from the eyes of many American animals more than once asserted in so distinguished a work as Rengger's Natural History of the Mammalia of Paraguay, and to find it there said, that this emission of light ceased on division of the optic nerves. But even this testimony cannot induce me to alter my conviction.

Some persons have imagined that the sensation of light produced by pressing the eye was also owing to the emission of light. But it is a mere sensation like that of pain in the skin, and is produced by any irritation of the retina, from whatever cause, whether from chemical, mechanical, or electric stimuli, or from an internal organic cause. The flashes of light perceived when the retina is thus irritated are unattended with any emission of light, and are, therefore, never visible to any other person than the subject of them.§

* See Schlegel, Beitrag zur nähern Kenntniss der Albinos; Meiningen, 1824, p. 70. † Esser, Kastner's Archiv. viii. 394. ‡ Tiedemann, loc. cit.

§ Compare my remarks on a medico-legal case, in which a person was said to have recognised a robber by the light produced by a blow on the eye. Müller's Archiv. für Anat. und Physiol. 1834, p. 140.

Note on the temperature of Insects.—I have been favoured by my friend, Mr. Newport, with the following interesting facts relative to the developement of heat in insects; they are extracted from a paper presented to the Royal Society on the 15th of June, and not yet published.

The amount of heat developed is proportionate to the quantity of the respiration; being, cæteris paribus, greater when the changes produced on the air by respiration are greater, and vice versâ. Berthold detected the evolution of heat only when several insects were collected together, not in one isolated from the rest. This must have arisen from his having ascertained the temperature only while the insect was in a state of rest; for Mr. Newport found that, although during such a state the temperature of the insect was very nearly or exactly that of the surrounding medium, yet, when the insect was excited or disturbed, or in a state of great activity from any cause, the thermometer rose, in some instances, even to 20° Fahr. above the temperature of the atmosphere,—for instance, to 91° when the heat of the air was 71°. The increase of heat is not dependent simply on the rate or velocity of the circulation as measured by the pulsations of the dorsal vessel; for in the earlier stage of the larva the amount of heat developed is less, while the frequency of the pulsations is greater; and at a later stage of the larva condition the frequency of the pulsations is less, and the heat greater, while at the same time the quantity of respiration, on which the evolution of heat really depends, is also increased.

Mr. Newport has observed, that a short time previous to each change, the temperature of the insect, as well as the frequency of the pulsations, and quantity of respiration, suffer a diminution.

SPECIAL PHYSIOLOGY.

BOOK THE FIRST.

Of the Circulating Fluids, their Motion, and the Vascular System.

SECTION I.

OF THE BLOOD. ITS GENERAL PROPERTIES.*

THE quantity of the blood in the body cannot be exactly determined: it is calculated, however, that in adult individuals it varies from eight to thirty pounds. It is the fluid from which are derived the materials for the formation and nutrition of all parts of the animal body. It takes up the effete materials from the different tissues for the purpose of their excretion by special organs, and is renovated by the new nutrient matters poured into it by the lymphatic vessels. These nutrient matters consist partly of substances introduced from without, and partly of matters which have already been organised components of the body. Their conversion into blood is effected not so much, probably, by the operation of particular organs as by the general action of all parts of the system upon them; for in the ovum, even before most of the organs exist, and when the first traces only of the central parts of the nervous system are formed, blood is generated within the area vasculosa by the germinal membrane, which is the cicatricula or germ more fully developed by the attraction and assimilation of the fluids of the ovum.

The blood which is brought to the heart from the lungs by the pulmonary veins, and projected by the left ventricle through the aorta and its branches into all parts of the body, has a *bright* red colour; that which returns through the venous system of the body to the right ventricle, and is thrown by it again into the lungs, has a *dark* red colour. The blood is also red in some invertebrate animals, as in the red-blooded

* On the blood generally, consult Parmentier and Deyeux in Reil's Archiv. b. i. heft. 2, p. 76. Hewson's Experimental Inquiries, 1772, in German, Vom Blute. Nürnb. 1780. Prevost and Dumas, Bibliothèque Universelle, t. xvii. p. 294. Meckel's Archiv. viii. Scudamore on the Blood, London, 1824, or über das Blut aus d. Engl. Würzburg, 1826. Berzelius, Thierchemie, 1831, or the 7th volume of his Traité de Chimie, translated into French by M. Esslinger. Denis, Rech. Experim. sur le Sang Humain, Paris, 1830. Thackray, Inquiry into the Nature of the Blood, London, 1819. Dr. G. Burrows, Croonian Lectures for 1834, in Medical Gazette.

worms. It has a reddish colour in some of the mollusca, at least in the planorbis, according to the observation of Treviranus and myself. In many invertebrate animals it is colourless.

If the blood is examined with the microscope either in the minute vessels of a transparent part, or immediately after it has flowed from the body, it is seen to consist of small *red particles* or *globules*, and a clear colourless fluid. This fluid is the *lympha* or *liquor sanguinis*, and must not be confounded with the serum, which is the thin fluid that separates from the crassamentum during coagulation. The liquor sanguinis can be obtained free from the red globules before coagulation takes place, by filtering the blood of the frog or some other animal in which the red globules are so large as not to pass through the white filter paper. The red particles are specifically heavier than the fluid, and consequently can contain no gasiform substance.

The specific gravity of human blood varies from 1·0527 to 1·057. It has a saltish taste, a weak alkaline reaction, and a peculiar odour,—halitus sanguinis,—which differs somewhat in different animals, and is strongest in the blood of the male sex.

The blood of all vertebrate animals usually coagulates within the period of from two to ten minutes after its escape from the vessel; the blood of the human subject requires from three to seven minutes for its coagulation, that of the rabbit two minutes only. It becomes first a gelatinous mass, which slowly contracts, and presses out a dirty yellow fluid,—the *serum*,—which appears first in drops on the surface, and gradually increases in quantity. The red coagulum is called *crassamentum, placenta, coagulum sanguinis*, or *clot.*

The *serum* has a specific gravity of from 1·027 to 1·029. It has a saltish taste, and in the higher animals has a weak alkaline reaction, which is scarcely perceptible in the frog. Herman was led into the error of supposing the serum to be acid, by observing that blood treated with tincture of litmus yields a reddish serum, which, however, arises from the red colouring matter of the globules being soluble in the tincture, just as it is in water. The serum holds in solution several animal matters, of which the chief is *albumen.* This substance requires for its coagulation the action of certain chemical agents, such as acids and alcohol, or a temperature of 158° Fahr.; it does not coagulate spontaneously.

If the red *coagulum* is washed for some time in water, the colouring matter is dissolved, and a white fibrous substance remains which is called *fibrin.* This substance, like the red clot, sinks in water unless it accidentally contains bubbles of air.

In females during pregnancy and in the puerperal state, in acute rheumatism and in inflammation,—indeed in all cases where the blood coagulates more slowly than usual,—the red globules often subside below the surface of the fluid before coagulation takes place, and the consequence

is, that afterwards, when the whole mass coagulates, the upper part of the clot is white,—forming the inflammatory crust or buffy coat,—while the lower part is red. When fresh blood is stirred quickly, the red globules are not included in the coagulum; the fibrin coagulates slowly into colourless fibres, which adhere to the rod with which it is stirred, while the rest of the blood remains fluid with the red globules floating in it. Fresh blood, if exposed to a very low temperature, freezes, and may in that state be preserved, being still susceptible of coagulation when it is thawed. Alkalies prevent the coagulation of the blood; even a thousandth part of caustic soda has this effect. Some salts also, as sulphate of soda, nitrate of potash, carbonate of soda, and carbonate of potash, when mixed with the blood out of the body, prevent or retard this phenomenon. Fontana states that the poison of the viper, and that of the ticuna, added in the proportion of one part to twenty parts of blood, have the same effect, while the viper's poison quickly induces the coagulation of the blood when inserted into a wound of the living body. There are certain circumstances, also, in which the blood remains fluid in the vessels, namely, in men and animals killed by lightning or strong electric shocks, in those poisoned by prussic acid, in animals hunted to death, and in men killed by violent blows on the epigastrum; and it is said that in these cases the limbs do not become rigid.

Except under the circumstances stated, blood, when removed from the body, always coagulates, whether it be kept at rest or in motion, whether it be placed in a temperature equal to that of the living body, in vacuo, in close vessels quite filled so as to exclude the air, or in various gases which do not form part of the atmosphere. [Dr. B. Babington* has shown that coagulation is *retarded* by exclusion of air, and to such a degree, that the red particles have time to subside. By letting blood flow into a vessel containing oil, he obtained a thick fibrinous covering, while a portion of the same blood received into an empty vessel formed no buffy coat.] The sole cause, therefore, of the coagulation is, that the proper combination of its elements is maintained so long only as the blood is under the influence of living surfaces, viz. of the vessels. [This requires explanation. Blood which is enclosed in a vessel between two ligatures, or of which the motion in the vessels has been impeded in any way, coagulates, though more slowly than out of the body; it seems necessary, therefore, not only that the blood should be in contact with living surfaces, but also that it should continue in motion.] Blood extravasated in the body, also, generally coagulates. Schroeder van der Kolk's† experiments seem to show that coagulation takes place with extraordinary rapidity after the brain and spinal marrow have been

* Medico-Chirurgical Transact. vol. xvi.

† Comment. de Sanguinis Coagulatione. Groeningen, 1820. Diss. sist Sang. Coagulantis Historiam. Gröning. 1820.

broken down; in a few minutes even after the operation, coagula were found in the great vessels. Mayer observed that, after the application of a ligature to the nervus vagus, the blood coagulated in the vessels, and death was thus produced. In four experiments, however, which were performed under my direction, two on dogs and two on rabbits, although the animals were examined immediately after death, which was the effect of this operation,—ligature of the nervus vagus,—in two cases only was a small coagulum of the size of a pea discovered in the left side of the heart, none in the pulmonary vessels. Hewson, Parmentier, and Deyeux, have observed that blood extracted from the vessels coagulates more rapidly in proportion as the vital powers of the animals decline. Several observers—Gordon, Thomson, and Mayer, for example,—declare that they have observed elevation of temperature during coagulation; while Dr. J. Davy* and Schroeder v. d. Kolk deny this most decidedly.

CHAPTER I.

MICROSCOPIC AND MECHANICAL EXAMINATION OF THE BLOOD.†

Of the Red Particles.‡

There is great want of accordance in the descriptions which writers have hitherto given of the red particles of the blood,§ I shall state here merely the results of my own observations.||

Mode of examining the red particles.—For the purpose of microscopic examination, the blood must not be diluted with water, for this fluid has the property of immediately changing the red particles from a flattened to a spherical form, and of rendering circular those which were elliptical. The blood should be either diffused very thinly over the surface of the glass, or diluted with some serum, or with a weak solution of common salt or sugar; these solutions produce no change in the appearance of the

* Tentamen experimentale de Sanguine. Edinb. 1814. Meckel's Archiv. i. p. 117. See also Meckel's Archiv. ii. 317, and iii. 454 and 456.

† From original researches. See Poggendorf's Annal. 1832. 8.

‡ [Considerable alteration has been made in the arrangement of the matter contained in this account of the red particles, for the sake of greater perspicuity.]

§ A full account of the observations of different physiologists will be found in E. H. Weber's edition of Hildebrandt's Anatomie, Bd. i. and in Burdach's Physiologie, Bd. iv. The best observers have been Muys, Fontana,—Nouvi Osservazioni sopra i globetti rossi del sangue, Lucca, 1766. Hewson,—Experimental Inquiries, pt. iii. Lond. 1777. Prevost and Dumas,—Biblioth. Univers. t. xvii. Meckel's Archiv. t. viii. R. Wagner,—Zur vergleichende Physiologie des Blutes, 1834.

|| [Professor Müller is evidently not aware that the most important facts stated in the following description of the red particles of the blood were ascertained long ago in this country, although they have since been much neglected. The translator has deemed it advisable to add a brief sketch of the labours of previous physiologists in the investigation of this subject.—See p. 107.

red particles. The method I adopt in examining these bodies in the blood of the frog is, to place a small quantity of the serum of the blood of this animal on the glass, and to add to it a small quantity of the blood. It is doubtless attributable to the use of bad instruments, and to the blood having been diluted with water, that the descriptions given of the red particles have been so various.

Their form in different animals is very various; but, whether they be elliptical or circular, they are always flattened.

In the mammalia, including the human subject, they are circular disks.* I have examined them in the calf, cat, dog, and rabbit, as well as in man, and am convinced that they are flattened in all these animals as well as in birds, reptiles, and fishes. It would be interesting to ascertain their form in the ornithorhynchus and echidna. In birds, reptiles, amphibia, and fishes, they are elliptic.† In some fishes they are more nearly circular, but never perfectly so.‡ In reptiles, amphibia, and birds, the long and short diameter of the red particles are about in the proportion of two to one.

It requires a good microscope to perceive the flattened form of these bodies in mammalia. When the diluted blood of a mammiferous animal is agitated under the microscope, many of the red particles roll over; and while placed on their edge are seen to resemble a short thick dark line, the extremities of which are not rounded, but cut off abruptly.§ They may be compared to a piece of money seen edgeways; but, in proportion to their long diameter, they are much thicker than a piece of money. In human blood their thickness is about one-fourth or one-fifth of their transverse diameter.

The flattening is greatest in reptiles, amphibia, and fishes; and of all animals is most remarkable in the salamander. In birds, also, the red particles are decidedly flattened; but not to so great a degree as in amphibia.

In the frog, the red particles—the thickness of which does not measure more than one-eighth to one-tenth of their long diameter—present, when seen edgeways, a slight prominence rising from the centre of each lateral surface, as Prevost and Dumas have represented. In other animals, even in the salamander, I have observed no prominence of this kind. R. Wagner, however, has observed it in many other animals, both reptiles and fishes.‖

* See Plate i. fig. 1. † See Plate i. figs. 2, 3, 4, 5, and 6.

‡ Rudolphi describes the red particles of fishes to be circular, and I formerly thought they were so in the clupea alosa; but it was before I was acquainted with the right method of examining them. The error arose probably from inaccurate observation, or from diluting the blood with water.

§ Plate i. fig. 1.

‖ Plate i. figs. 2, 3, 4, 5, and 6.

Central spot.—In the centre of each red particle is a spot, which in the circular bodies is circular, in the elliptic also elliptic; on the illuminated side of the particle it appears light, on the opposite side dark. This spot has sometimes—I may say, indeed, has always in the elliptic globules, — the appearance of being produced by a central nucleus, especially when the particle is brightly illuminated, and all shadow avoided. By a less brilliant light this central spot suggests rather the idea of an elevation; and this is particularly the case in the frog. It has not at all this appearance in the salamander, nor in birds, nor fishes. The apparent elevation in the red particles of the frog's blood is most marked when the quantity of serum in which they are contained is small, and then it looks as if it were surrounded by a depression between it and the outer ring.* These, I say, are the appearances presented under certain circumstances: I give no opinion as to their mode of production. But as the red particles in birds, salamanders, and fishes, generally present no appearance of an elevation on their flat surfaces when they are rolling over on their edge under the microscope, it is evident that in them this central spot cannot be produced by an elevation, and must be referable to the central nucleus, which all these bodies contain. And the slight lateral prominence observed in the particles of frog's blood, and, by Wagner, in those of many other animals, when seen edgeways, must also be attributed to the central nucleus.

In the red particles of mammalia, the central spot never appears elevated. It is from writers having assumed that what they observed in one animal existed also in others, that so much confusion with reference to this subject has been produced. In many points, however, I have found the observations of Prevost and Dumas correct. In mammalia, the red particles have sometimes, by a certain light, the appearance of being very slightly excavated from the border towards the centre†. Dr. Young is inclined to regard this appearance as a real depression of the surface: this, however, seems to me to be very improbable; for I have satisfactorily ascertained that each of these bodies contains a small nucleus, equal in thickness to the red particle itself. When the red particle of mammalia is placed obliquely, so that part of one surface and part of one border meet the eye, the upper border forms a dark semicircle, convex in one direction, and concave in the other. I will presently detail experiments by which I am able to demonstrate the existence of a nucleus, with chemical characters perfectly different from those of the outer vesicle, in each of the red particles of the frog and salamander. And as this nucleus has under the microscope exactly the same appearance in the red particles of birds and fishes as in those of amphibia, it would be expected to exist in those of mammalia also.

* See Plate i. figs. 2 and 3. † See Plate i. fig. 1.

And although, on account of the minuteness of these bodies in mammalia, it is more difficult to demonstrate the nucleus in them, I have with an excellent (Fraunhofer) microscope really seen it, and distinctly. Even in the red particles of human blood, I have seen a minute, round, accurately-defined nucleus, which had a more yellowish and shining aspect than the transparent part around it. The existence of the nucleus can also be demonstrated by the action of acetic acid, though much less distinctly than in the case of frog's blood.

The size of the red particles in human blood is pretty uniform; some few are larger, but none have twice the diameter of the majority. In the frog also their size is for the most part equal; some, however, without differing in any other respect, are somewhat smaller than the rest, and appear to be, as it were, in the process of formation. Prevost and Dumas have found the red globules in the embryo to be larger than those of the adult animal. In the embryo of the rabbit their dimensions are very unequal; the greater number are quite as large as in the adult, and a few are more than twice that size. In the tadpole the same bodies appear to be somewhat smaller than in the frog, and are much paler.

The red particles of amphibia are the largest that I am acquainted with; in birds, reptiles, and fishes, they are smaller; in mammalia smallest, and among mammalia those of the goat are the most minute, as Prevost and Dumas correctly observed. In the calf they are rather smaller than in man. The red particles of frog's blood being taken as a standard of comparison, and observed under the microscope side by side with those of other animals, it is found that those of birds are about one-half the size of those of the frog; that the red particles of the salamander are somewhat larger, not so much as one-third larger than those of the frog, they are rather more elongated; those of the lizard compared with the same bodies are found to be about two-thirds the size, while the circular particles of human blood measure only one-fourth the long diameter of the elliptic particles of frog's blood. The red particles in man I have found to measure from 0·00023 to 0·00035 of an inch French in diameter.

[From the following table it will appear that the measurements of the red particles given by different physiologists, with the exception of Sir E. Home and Mr. Bauer, are all within or nearly within the limits assigned by the author.

	Parts of an English inch.
Dr. Young	$\frac{1}{5000}$
Captain Kater	$\frac{1}{4000}$ to $\frac{1}{6000}$
Dr. Wollaston	$\frac{1}{5000}$
Sir E. Home and Mr. Bauer	$\frac{1}{1700}$
Prevost and Dumas	$\frac{1}{3690}$
Dr. Hodgkin and Mr. Lister	$\frac{1}{3000}$
Professor E. H. Weber	$\frac{1}{4615}$

	Parts of an English inch.
Professor R. Wagner	$\frac{1}{4430}$ to $\frac{1}{3323}$
M. Milne Edwards . . .	$\frac{1}{3900}$
Professor Müller	$\frac{1}{4029}$ to $\frac{1}{2637}$

The following table, showing the size of the red particles in the blood of different vertebrate animals, is derived from Professor Wagner's treatise, a few examples only of each class having been selected.]

Name of the animal.	*Name of observer.*	*Size in fractions of an English inch.*	
In mammalia.		Diameter.	
Simia callitrix .	Prevost and Dumas . .	$\frac{1}{3048}$	
Cat . . .	Do. . . .	$\frac{1}{7056}$	
Ox . .	Wagner . . .	$\frac{1}{4430}$	
Goat . . .	Prevost and Dumas .	$\frac{1}{4226}$	
In birds.		Long diameter.	Short diameter.
Common fowl .	Wagner . .	$\frac{1}{1681}$	$\frac{1}{2769}$
Do. . . .	Prevost and Dumas .	$\frac{1}{2038}$	$\frac{1}{3810}$
Goose, Raven, House-sparrow, and Goldfinch.	Do. . .	$\frac{1}{2184}$	$\frac{1}{3810}$
In reptiles.			
Land tortoise . .	Prevost and Dumas .	$\frac{1}{1219}$	$\frac{1}{1955}$
Do. . . .	Wagner . .	$\frac{1}{1384}$	$\frac{1}{1938}$
Coluber berus . .	Prevost and Dumas .	$\frac{1}{1524}$	$\frac{1}{2540}$
Lacerta agilis .	Wagner . .	$\frac{1}{1292}$	
In amphibiæ.			
Salamandra cincta et cristata . .	Prevost and Dumas .	$\frac{1}{889}$	$\frac{1}{1422}$
Rana bufo, esculanta, temporaria .	Do. . .	$\frac{1}{1193}$	$\frac{1}{1905}$
Rana esculanta .	Wagner . .	$\frac{1}{1107}$ to $\frac{1}{997}$	$\frac{1}{1292}$
In fishes.			
Lophius piscatorius .	R. Wagner .	$\frac{1}{1938}$	
Squalus squatina .	Do. . . .	$\frac{1}{1107}$ to $\frac{1}{886}$	

Chyle globules in the blood.—In the blood of the frog as obtained from the heart of the animal, I have found other smaller bodies, much less numerous than the red particles, about one-fourth their size, and perfectly spherical. They agree in every respect with the scanty globules seen in the lymph of the frog, which will be described in a future section; and are evidently identical with them, being poured into the blood with the lymph and chyle.

[Hewson* observed these lymph globules in the blood, and believed that they were identical with the nuclei of the red particles. He

* Hewson's Experimental Inquiry, p. 133.

supposed that the nuclei are formed in the lymphatic glands, and that the red envelope is afterwards found around them, chiefly by the spleen.]

It is possible that the nuclei of the elliptic particles are derived from these lymph globules. The nuclei freed from the covering of colouring matter are of about the same size, but they are elliptic in form, and in the salamander distinctly flattened, while the lymph globules are spherical. In mammalia, too, the globules of the lymph and chyle are much larger than the nuclei of the red particles in the same animals; and from the entire red particles they differ, in being perfectly insoluble in water, while the red particle, with the exception of its minute nucleus, is soluble in that fluid.

It is generally believed that the conversion of the chyle into blood is effected very quickly. Such may certainly be the case; but the difficulty of distinguishing the chylous globules in the blood is sufficiently explained by their being diffused among the more numerous red particles. During the ordinary coagulation of the blood of man or mammalia generally, the chylous globules are included in the crassamentum with the much more numerous red particles, and the serum is left transparent; but if coagulation is retarded by the addition of a minute proportion of carbonate of potash, the red particles subside, while the chylous globules being lighter are suspended in the upper part of the fluid, rendering it milky.

Different action of serum and water on the colouring envelope.—Sir Everard Home* speaks of the red particles undergoing rapid decomposition; this is quite incorrect. The blood of a mammiferous animal from which the fibrin has been removed by brisk stirring, retains all the appearance of fresh blood, and the red particles remain suspended in it, with no change of their form or size discoverable by the best microscope after the lapse of several hours, or even on the following day. At the end of twenty-four hours, although they have then subsided several lines below the surface of the fluid, no perceptible solution of their red envelope has taken place; the supernatant serum is still yellow, and untinged by the red colouring matter. In the blood of sheep and oxen, thus deprived of fibrin, the red particles subside $1\frac{1}{2}$ line in the course of from twelve to twenty-four hours, and after being kept several days at a temperature of 59° Fahr. the depth of the supernatant fluid left free from red particles by their subsidence is not more than $2\frac{1}{2}$ lines, and the fluid is but very slightly tinged. In human blood, and in that of the cat, the red particles subside somewhat more rapidly, namely, as much as four or six lines in a few hours. In the serum of frog's blood, they subside very rapidly, but nevertheless, they preserve their form and size unaltered for several days, if the atmosphere is not very warm.

But if water be added to such a mixture of the red particles and

* Philos. Trans. 1818.

serum of the blood of a mammiferous animal, a part of the colouring matter is quickly dissolved, and a large portion of the red particles sink to the bottom of the vessel. The further effects of water on the red particles are best observed in a mixture of the serum and red particles of frog's blood. Such a mixture I obtain by removing each portion of coagulum as it forms, having first agitated it a little in the serum to separate any adherent particles. By this means a considerable number of the red particles are left in the serum, although many are removed in the coagulum. Thus prepared, the blood of the frog is adapted for many microscopic experiments on the changes produced in the red particles by different substances; experiments for which fresh blood cannot be used on account of the coagula which form in it.

Nuclei.—If such blood is mixed with water, the colouring matter of the red particles is dissolved. To accelerate the solution, the water should be added in considerable quantity. The solubility of the colouring matter in water enables us to demonstrate the existence of a nucleus in each of the red particles. For this purpose a watch-glass should be filled with a mixture of this blood and water, and after waiting a short time for the particles to subside, the whole should be immersed in a large glass vessel partly filled with water, taking care not to disturb the sediment in the watch-glass. After standing for eighteen or twenty-four hours the red deposit will have become white, and, if some of it be examined with a microscope, the elliptic red particles will no longer be seen, but in their place a great number of small bodies, not more than a fourth the size of the original red particles, and for the most part roundish in form, a few only oval. If the sediment is examined at intervals during the period mentioned, it will be quite apparent that, in proportion as the water becomes tinged with the colouring matter, the elliptic particles lose their red envelope, and become smaller and smaller until the colourless nuclei merely remain. These nuclei are not further soluble in water, but form at length a mucous matter at the bottom of the glass, still consisting of the same granules. The nuclei of the red particles cannot be demonstrated in this manner in human blood on account of their minuteness; but from analogy it is probable that, when human blood is treated as above, the nuclei of its red particles also remain undissolved, but are suspended in the water. When the blood of mammalia coagulates, the red particles are included in the clot; and when the red colouring matter is extracted by washing in water, the nuclei may still remain in the fibrinous mass, or they may be separated from it, becoming suspended in the water, but they are not dissolved.

Effects of different re-agents on the red particles.—The nature of the red particles of the blood is much elucidated by the changes produced in them by the action of various fluids. To watch these changes a good

compound microscope is required, and the blood of the frog or salamander must be employed. A drop of the frog's blood freed from the fibrin, and a drop of any fluid of which we desire to try the effect, should be placed side by side upon a plate of glass, and the two drops made to unite, the effects produced at the moment that they become mixed being watched by means of the microscope; or the red particles may be first examined separately, and again after the re-agent has been added. This is the method I have constantly adopted in the following experiments.

Water.—The instantaneous effect of water on the red particles is very remarkable. Those of human blood become indistinct; the further changes that they suffer cannot be distinguished with accuracy, on account of their minute size; I think, however, that they are rendered globular, for, while they were floating about under the microscope, I could perceive none with a sharp border. But in the blood of the frog every change is distinctly seen. The elliptic bodies immediately become globular, no longer presenting a sharp edge to the eye as they roll over in the fluid. Whether they are enlarged at the same time, I cannot determine; their diameter is now intermediate between the long and short diameter of the ellipsis which they before presented Many appear unequal in size, are uneven on the surface, and of irregular form; the majority are globular, but not accurately so. In several the nucleus is displaced, is no longer at the centre, but at the side; in a few it is wholly wanting; in these it seems as if the violent change produced in them by the water had caused the expulsion of the nucleus, for, besides these globules which have lost their nuclei, a few nuclei without envelopes can also be seen strewed over the field of the microscope. These free nuclei are distinguished from the smaller globular or chylous particles of the frog's blood, already described, by their elliptic form. More water being added, the red particles gradually diminish in size, dissolving away, till at length nothing but the insoluble nuclei remain. Water in which carbonate of potash, common salt, sal ammoniac, or sugar has been dissolved produces no change in the size and form of the globules, unless it be a saturated solution of carbonate of potash, which seems to produce a slight and gradual diminution of their size.

Water, as Berzelius remarks, dissolves the colouring matter in all proportions. Prevost and Dumas had denied this; but the experiments just described, particularly those performed with frog's blood, prove, beyond doubt, that the colouring matter is really dissolved, and not suspended in minute particles in the water.

Berzelius seems to attribute the insolubility of the colouring matter in serum to the albumen, which this fluid contains. But I cannot think that this is the sole cause, and believe this property of the serum to be chiefly owing to the salts which enter into its composition; for when

I added to a small quantity of the frog's blood under the microscope a solution of yolk of egg, the change in the red particles from the flattened to the spherical form, took place as rapidly as when I added pure water; but when, in place of the solution of yolk of egg, I added a watery solution of any salt which produces no chemical change in the blood, such as carbonate of potash, or common salt, the form and size of the red particles were not in the slightest degree altered.

Acetic acid.—If, instead of water, dilute or concentrated acetic acid is used, the elliptic particles immediately become irregular in form, and some are rendered globular. The red colouring matter is in a few minutes almost entirely dissolved, leaving small bodies not more than one-third or one-fourth the diameter of the original red particles. These are not globules contracted by the action of the acid, but nuclei deprived of the red colouring matter. The colouring envelope is not however wholly dissolved, for with the Fraunhofer microscope I could still distinguish a delicate exceedingly pale line, surrounding the central nucleus. The outline of these bodies is the same as that of the red particles; in those obtained from frog's blood I could not distinguish any flattening, but those from the salamander's blood are as distinctly flattened as the red particles themselves. The length of the nuclei from frog's blood is the double of their breadth; some few, however, approach the circular form. In the red particles of the salamander, the nuclei are more elongated, their lateral borders are almost parallel, while their extremities are rounded. By means of acetic acid, the extremely minute nuclei of the red particles of the blood of mammalia can be rendered visible, but the most careful manipulation and a very clear instrument are required for the experiment.

If the blood of the frog freed from fibrin be mixed in some quantity with acetic acid, the same change in the globules takes place; but we also observe that the nuclei subside in the form of a light brown powder, which, after the lapse of several days, remains undissolved, and which is found even at a later period, if examined by the microscope, to consist of the unaltered nuclei of the red particles. Fibrin and albumen are not rendered brown by the action of acetic acid; on the contrary, it renders them transparent, and by degrees in part dissolves them. The brown colour of the deposit, therefore, seems to depend on some of the colouring matter which still adheres to the nuclei, and is perhaps chemically changed; for the nuclei obtained by subjecting the red particles to the action of a large quantity of water are white, and remain so when acetic acid is poured over them. The acid used in these experiments was ascertained to be pure, and was somewhat more concentrated than the acetic acid of the Prussian pharmacopœia.

Muriatic acid does not dissolve all the colouring envelope; it diminishes the size of the red particles very slightly. *Chlorine* destroys the

colour; the frog's blood becomes first brown, afterwards nearly white, like milk: the albumen at the same time coagulates into globular granules. If this white matter is examined by the aid of a microscope, the form of the elliptic particles of the blood can still be distinguished in it, but they are somewhat smaller. The experiment may be made in two ways; either the chlorine may be passed through a tube moistened internally with the blood, or the blood may be poured into a very narrow-necked glass jar filled with chlorine. In the latter case the blood flows a short way down the side of the jar, but soon coagulates.

The form of the red particles is not affected by *oxygen* or *carbonic acid.*

Liquor potassæ dissolves the red particles very quickly,—the nuclei as well as the colouring envelope, — without previously changing their form. The solution is effected still more rapidly by *liquor ammoniæ,* and is also complete; but at the moment of mixture the red particles become globular. *Alcohol* merely produces slight contraction of them; and the globules of albumen, produced by the coagulation of the serum, cloud the field of vision and render the red particles indistinct. *Strychnine* and *morphia* produce no change in them.

The size and form of the red particles are the same in *arterial* and *venous* blood. This is contrary to the statement of the otherwise accurate Kaltenbrunner, who describes them as increasing somewhat in size, and losing their defined border, which is dissolved away, as it were, in their passage through the capillaries. I also found that no change was produced in the form of the red particles of the frog, when I tied the lungs at their root and cut them out; the animal still lived thirty hours, probably from respiration being carried on by the skin, as it was in the fishes in Humboldt's and Provençal's experiments.

[*Historical account of the red particles.*—The existence of the red particles in the blood was discovered by Malpighi, and shortly afterwards by Leeuwenhoeck,* in 1673, who thought that their form in mammalia was globular, although he recognised their flattish and oval form in birds, reptiles, and fishes. The representation that he has given of these bodies in fishes is interesting, inasmuch as it proves that he had observed the oval spot in their centre. Passing by the observations of M. de la Torre,† which are unworthy of notice, the account given of the red particles of the blood by Mr. Hewson,‡ in 1774, next claims our attention. This able observer ascertained, with certainty, that they are flattened in man and quadrupeds, as well as in the other vertebrate classes; and he found that their flattened form is equally distinct in the living animal (for instance, in the web of the frog's foot), as when removed from the body. He observed that their size does not correspond with the size of the animal, but is smaller in quadrupeds than in birds, and in birds than in fishes, and that they are larger in the young of the viper and common fowl than in the adult animals. Hewson knew the advantage of diluting blood with serum. His experiments to prove that the central spot is produced by a solid nucleus are particularly interesting, since they show that he was fully aware of the changes produced on red particles by the action of water. He describes their change from a flattened to a spherical form, when water was added; the gradual thinning of the

* Phil. Transact. 1674 and 1684. † Phil. Trans. 1765. ‡ Loc. cit.

external vesicle till merely the middle globular and very small particle was left. This nucleus, he observes, is less easily soluble in water than the envelope. The property which serum possesses of not dissolving the red particles or altering their shape, Hewson attributed chiefly to its saline ingredients, and proved by experiment that solutions of neutral salts, if not too concentrated, have the same property as serum in this respect, and are equally well adapted for diluting the blood in microscopic experiments. He observed that concentrated solutions of salts produce contraction and shrivelling of the vesicles. Other of Hewson's observations have not been confirmed.

Dr. Young* published, in 1818, a concise account of his microscopic examination of the red particles. He confirmed Hewson's remarks as to the existence of a nucleus in the particles of the blood of the skate, but believed that in those of human blood there is no nucleus; on the contrary, that their form is that of a doubly concave lens; although he remarks that the apparent central depression on each surface may depend on some internal variation of refractile density.

The appearance of a central depression had been previously seen by Fontana,† for in all the figures which he gives of these particles, the line which surrounds the central bright spot is darkest on that side which is most illuminated. But he paid no attention to this circumstance.

The statements contained in the memoirs of Sir E. Home‡ and Mr. Bauer, on this subject, were nearly all erroneous. These observers added nothing to our knowledge of the bodies, but unfortunately were too willingly credited, and caused the more accurate observations of Hewson to be neglected.

The subsequent researches of MM. Prevost and Dumas § tended in part to confirm the views of Hewson, namely, as to the flatness of the particles and their consisting of a nucleus and enveloping coloured vesicle. They first perceived a slight prominence in the centre of the lateral surface. But in some respects their statements more nearly coincide with those of Sir E. Home and Mr. Bauer, and here they are obviously in error. Thus they suppose that during coagulation the red particles lose their colouring envelope, and that the nuclei then coalesce. They believe that the red vesicle falls to pieces when acted on by water, without being dissolved; and they even give a drawing of a red particle of the blood of the salamander, which had been some days in water, and of which the envelope had burst and the nucleus not escaped. The immense magnifying power with which this was viewed, namely, 1000 diameters, would excite a doubt as to the accuracy of the observation, and this doubt is strengthened when we consider that all the best observers agree as to the solubility of the external coloured portion of the particles in water.

By varying the mode of observation, Dr. Hodgkin and Mr. Lister‖ endeavoured to prove the correctness of Dr. Young's opinion that the red particles of human blood have each the form of a doubly concave lens. They think that this is demonstrated, 1. by the circumstance that the image of any opaque body placed between them and the light, is transmitted in an inverted position, precisely as would be done by a concave lens; 2. by the appearance presented by the particles when viewed dry as opaque objects; and 3. by the appearance of two concave surfaces when the particle is seen at right angles to the surface of the glass in the focus of the lens.

The originality of Professor Müller's investigation of these bodies consists principally in his employing blood from which the fibrin had been removed; and in his ascertaining the action of different substances, particularly the gases, upon them. The property of serum and saline solutions was known to Hewson, who also knew well the

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* Medical Literature. † Traité du venin de la Vipère. ‡ Phil. Transact. 1818.

§ Loc. citat.

‖ In their translation of Dr. Edwards, on the influence of physical agents on Life, Appendix, p. 432.

effect of the admixture of water; while Dr. Milne Edwards had, in 1826,* observed that acetic acid strips the red particles of their envelopes and leaves the nuclei isolated.

Professor Wagner's† account of the red particles in the vertebrate classes are chiefly confirmatory of the observations of preceding physiologists; but he extended his observations to a greater number of species. He observed the central elevation in birds, reptiles, and fishes: in reptiles he found this elevation generally less prominent than in birds: in all the vertebrate classes the border is generally cut off abruptly, but in some fishes it appeared to be sharp, the central prominence rising gradually from it.

Wagner has also examined these bodies in the different classes of the invertebrata. He found that whatever the colour of the blood might be, the particles floating in it were always roundish, not regular in form, but generally granular on the surface.‡ During the circulation, these particles underwent great changes of form. In some invertebrate animals a number of small granules or nuclei are seen in the interior of the blood particles. In the blood of some animals the particles are very scanty; Wagner formerly supposed that they were entirely wanting in some species, and instanced the hirudo vulgaris; but he has since found them in this animal. They are most numerous in the blood of cephalopods and ascidiæ, but even in them they are less abundant than in the vertebrate animals. The following table is sufficient to show that the size of these bodies varies very much in the different invertebrate animals as well as among the vertebrata.

Name of animal.	*Observer.*	*Greatest diameter. In fractions of an English inch.*
Maja squinado	Wagner	$\frac{1}{2807}$ to $\frac{1}{1938}$
Scorpion	Do.	$\frac{1}{2215}$ to $\frac{1}{1938}$
Larva of ephemera	Do.	$\frac{1}{3323}$ to $\frac{1}{2215}$
Terebella	Do.	$\frac{1}{2215}$ to $\frac{1}{553}$
Octopus moschatus	Do.	$\frac{1}{2769}$ to $\frac{1}{2215}$
Helix pomatia	Prevost & Dumas	$\frac{1}{2769}$
Astirias aurantiaca	Wagner	$\frac{1}{5538}$ to $\frac{1}{1661}$]

Of the liquor sanguinis.

The *liquor sanguinis*,—the fluid portion of the blood in which the red particles float during life,—separates, when coagulation takes place, into two parts,—the *serum*, and the *fibrin* which was previously in solution. The fibrin coagulating encloses within it the red particles. The serum still retains the albumen in solution. We shall treat first of the *fibrin*.

1. *Of the fibrin.*

It is generally supposed, that the coagulation of the blood results from the aggregation of the red particles. These bodies are thought to be merely globules of fibrin in an envelope of red colouring matter, and it is imagined that the clot is formed of these red particles, and is rendered white by washing, from the red envelopes being removed from the particles so as to leave merely the nuclei of fibrin. This explanation of the process of coagulation was proposed more especially by Sir Everard Home and by Prevost and Dumas. It has been presupposed also by Dutrochet in his late investigations on the action

* Ann. des Sciences Nat. t. ix. † Loc. citat.

‡ See the representation of the corpuscules in the blood of the scorpion, Plate i. fig. 7.

of galvanism on the blood. Berzelius, observing that lymph contains fibrin in solution, conjectured that the blood also must contain it in that state; because, he says, the lymph is a fluid separated from the blood: a still stronger reason might be adduced,—namely, that the lymph is poured into the blood. Berzelius, therefore, suggested that the clot was formed by the fibrin coagulating and enclosing the red particles. This idea of the fibrin being in the state of solution in the blood has been advanced several different times. I have been so fortunate as to discover a definitive proof of Berzelius's conjecture.*

In some frog's blood which had been received into a watch-glass, I observed that before the whole mass coagulated, some colourless transparent clots formed, which I could draw to the edge of the glass with a needle; and on pouring off the blood, one or two minutes after it had flowed from the animal, I perceived that there were points or small fragments of similar coagula remaining adherent to the bottom of the glass. To this experiment it might be objected that in amputating the frog's thigh, which is the readiest mode of obtaining blood from this animal, some lymph had escaped with the blood, and had given rise to these coagula; I therefore collected the blood for the future directly from the great ischiadic artery, which runs among the muscles at the posterior part of the thigh. I laid bare this artery, which is easily found, on account of its running close to the great ischiadic, or crural nerve, as it is usually called, and collected the blood from the artery only, and with such care as to be sure that I had pure

* [In England this has not merely been the opinion of individuals, but, before physiologists were led astray by the incorrect observations of Sir Everard Home and Prevost and Dumas, it was the opinion generally held and taught in the schools. Thus Mr. Hewson, speaking of the constitution of the blood, does not assert it as his own discovery; he says, "*It is well known* that the crassamentum consists of two parts, of which one gives it solidity, and is by some called the fibrinous part of the blood, or the gluten; but by others more properly termed the coagulable lymph; and of another which gives the red colour to the blood, and is called the red globules." Dr. Gordon also, in his Syllabus of Lectures on Anatomy, describes the blood to consist of the fluid portion and of the red portion, and the fluid portion to consist of the serum and lympha; and I am informed by Dr. Sharpey that Dr. Gordon was in the habit of giving this description of the blood in his lectures, not as the result of a new discovery, but as the general opinion of physiologists.

As to the proofs on which this opinion rested, much more had certainly been done than Professor Müller supposed. Hewson, who was acquainted with the effects of neutral salts in retarding the coagulation of the blood, observed, (p. 11, Experimental Inquiry,) that when a salt, such as Glauber's salts, is mixed in considerable quantity with the blood, the red particles subside, and the surface of the mixture becomes clear and colourless, and that this clear fluid can be poured off from the red part, and is found to contain coagulable lymph, which coagulates on the addition of water. He observed (p. 35), that "in inflammation the surface (of the blood) became transparent, that the transparency went deeper and deeper, the blood still remaining fluid:" he removed a part of the clear liquor with a wet tea-spoon, and put it into a phial

blood. I obtained blood in the same way from the heart, which is done with more facility. In this blood, of the purity of which there could be no doubt, the same small transparent coagula were always formed before the entire mass of blood coagulated. A drop of this pure blood was diluted with serum, and placed under the microscope. The globules then appeared widely separated, but in the spaces between them I could discern the formation of a coagulum which connected these bodies together, however wide the intervals between them; and by placing a needle between any two globules, and moving it about, I could set the whole mass in motion. As the red particles of the frog's blood appear very large when viewed by a high magnifying power, this experiment admits of the greatest accuracy, and is perfectly convincing.

There is, however, another much easier, and indeed still more unquestionable method of demonstrating the same fact. Knowing that the red particles of frog's blood are four times the size of those bodies in the blood of mammalia, I conjectured, that, although the red particles of the latter animals pass through filter paper, those of the frog might not: I found this opinion correct. Thus, as generally happens, the most simple means was the last thought of. I am now enabled to show at lecture by an easy experiment, that fibrin is held in solution in the blood; that it passes limpid through the filter, and then coagulates. The experiment can be made quite on a small scale with the blood of a

with an equal quantity of water, a second portion he kept in the tea-spoon; "both these portions, as well as the surface of the larger mass of blood, coagulated; the portion in the tea-spoon, when compressed, yielded serum." He observed also that inflammatory blood coagulates more slowly than healthy blood (p. 49): "May we not conclude, therefore," he says, "that in those cases where the inflammatory crust appears, the coagulable lymph of the blood is thinner, and its disposition to coagulate lessened? both of which circumstances contribute to the subsidence of the red globules from the surface of the blood, which then coagulates." And again: "This remarkable appearance might be accounted for by supposing that the lymph had ascended to the surface of the blood in those cases; but this is improbable from considering that in its coagulated state it is of greater specific gravity than the serum and sinks in it?" These passages show that Hewson had no doubt in his mind as to the state in which the fibrin exists in the blood. But still his proofs are defective in one point; he did not show that the red globules still preserved their perfect state when the fibrin separated, and that the fibrinous transparent portion of the blood did not contain colourless globules; that the fibrin consequently was independent of the red particles. In this respect the merit of the *definitive* proof is certainly due to Professor Müller. Mr. Hewson knew that the crassamentum contained red particles in their perfect state, for it was by agitating crassamentum in the serum that he obtained the red particles for observation, but this did not prove that all were unchanged. Professor Müller, by his experiment of filtering the blood before coagulation, has proved that the fibrinous portion contains no globules, and has shown that, when the fibrin is removed, the red particles can still be seen by the microscope all in their perfect state.]

single frog; a small glass funnel and a filter of common white filter paper, or not very thick printing paper, are all the apparatus required. The filter must of course be previously moistened; and it is better to add some water to the blood as soon as the latter is poured into the filter. What then passes through is a perfectly clear serous fluid diluted with water, and merely tinged in the slightest degree by the red colouring matter, which in frog's blood is not rapidly dissolved. Sometimes it is quite colourless. If, in place of pure water, a very dilute syrup—containing one part of sugar in two hundred or more parts of water—is employed, the red envelope of the particles is not at all acted on, and the filtered fluid is perfectly colourless. No globules can be discerned in this fluid by the aid of the microscope. In a few minutes a coagulum forms, which on account of its transparency would not be remarked, were it not drawn out of the fluid with a needle. This coagulum gradually contracts, becomes whitish and fibrous, and then has exactly the aspect of human lymph.* The fibrin of the blood is by this means obtained in a purer state than is possible by any other method. Of course all the fibrin of the blood is not obtained by this process; the greater part of it coagulates before it can pass through the filter. To find the paper best adapted for the filter, some trials must be made with different kinds. If the paper is too thin, some few red particles pass through it with the fluid, and will afterwards be seen here and there in the coagulum. If the paper be of the proper thickness, the coagulum will not contain a single red particle. There is no distinct appearance of granules in the fibrin thus obtained; it is quite homogeneous; when it has contracted and become white, it acquires a finely granulated aspect. This appearance, which it presents when viewed with the compound microscope, may, however, arise merely from unevenness of the surface.

There is still another mode of proving that fibrin exists dissolved in the blood of the frog as well as of mammalia. By adding to the blood of man or any vertebrate animal some drops of a very concentrated solution of carbonate of potash, coagulation is retarded, so that the red particles have time to subside. In the space of half an hour a soft coagulum forms, of which the lower part containing the red particles is red, while the upper part is white.

Proportion of fibrin in the blood.—We are indebted to MM. Prevost and Dumas for an attempt to calculate the amount of the red particles in the blood of different animals from the weight of the crassamentum when dried. However, as Berzelius has remarked, the result of such calculations can never be exact, because the crassamentum contains a large quantity of serum, the albumen and salts of which must be left behind during desiccation; and if the coagulum were washed,

* See Book i. Section iii. on the Lymph.

not only the serum, but the red colouring matter also would be removed. It must likewise be remembered, that Prevost and Dumas consider the fibrin to be wholly derived from the red particles, so that what they speak of as the amount of red particles, must be regarded as the sum of the red particles and fibrin together. With this correction, their numerous calculations of the proportional weight of the different component parts of the blood are of value. These remarks apply also to the otherwise excellent researches of Lecanu with regard to the quantity of the red particles in the different temperaments and sexes.

To determine the quantity of fibrin in the blood of different animals and in different diseases, new experiments are required. The best mode of ascertaining the quantity of fibrin is briskly stirring the blood with a rod or bunch of twigs, when the fibrin separates in the form of a colourless or nearly colourless coagulum, and leaves the blood of its natural colour; the red particles floating in it having undergone no change, provided that water had not been added.* This is the only method by which the red particles can be separated in their perfect state from the fibrin. If the fluid parts are strained off through a linen cloth, and the solid fibrin washed so as to purify it from serum, the weight of fibrin contained in a certain quantity of blood can be accurately determined. The exact proportion of red particles cannot be ascertained. The weight of fibrin deducted from the weight of crassamentum ascertained to be formed from the same quantity of blood, say one hundred parts, will leave a remainder, which will indicate the quantity of red particles, together with the albumen and salts contained in the coagulum. The proportion which the albumen bears to the red particles may be ascertained by finding the weight of albumen in a certain proportion of serum; and then, after removing the fibrin from some blood of the same animal, evaporating the blood

* Berzelius (Traité de Chimie, tom. vii. Chimie Animale) remarks that when blood, which has been deprived of its fibrin in this way, is examined under a compound microscope, the red particles are no longer visible; but in their place small comminuted fragments, which he regards as portions of the pellicle of colouring matter, are seen floating in a yellowish fluid. They pass through the filter paper, he says; but so do the red particles of the fresh unstirred blood of the higher animals. Berzelius further states that when blood is kept several days in a temperature of 32° Fahr. these red fragments slowly subside and leave the supernatant fluid quite clear, although sometimes this fluid is reddened by a little of the colouring matter being dissolved. Notwithstanding the high respect I entertain for this great man, I must say that the red particles of blood which has been deprived of its fibrin by stirring, always appear to me to preserve their perfect form unless water had come into contact with them. I have examined these bodies in the blood of the calf, ox, cat, and man, previously freed from its fibrin in this way, and have never found them altered in any respect, their flattened form being as distinct as in the fresh blood.

to dryness, and observing the weight of the water lost. Now admitting that this water, and consequently the water with which the red particles were impregnated, contained the same proportion of albumen as the serum, the weight of the albumen left in the residue after the desiccation of the blood freed from the fibrin may be easily calculated; and, by deducting its weight from that of the whole residue after desiccation, the quantity of the red particles will be found. This is the method Lecanu appears to have adopted in determining the proportion of the cruorin, but it rests on a mere supposition.

The only point which I have investigated, is the proportion of fibrin in the blood, this being the only one which can be determined with accuracy. From 3627 grains of bullock's blood I obtained, by stirring, 18 grains of fibrin. The crassamentum of 3945 grains of the same blood weighed, when dried, 641 grains. So that in 100 parts of the blood of this animal there were 16·248 parts of dry crassamentum and 0·496 parts of fibrin. Fourcroy estimates the quantity of dry fibrin in 1000 parts of blood at from 1·5 to 4·3. Berzelius calculated that it was 0·75; while Lassaigne found it to be 1·2. In twenty-two experiments Lecanu found, that the proportion of dry fibrin in 1000 parts of human blood varies from 1·360 to 7·235 parts.*

Proportion of fibrin and red particles in arterial and venous blood.—Prevost and Dumas state, as the result of their experiments, that arterial blood contains more red particles than venous blood; meaning of course that it contains more crassamentum. Arterial blood would be expected to contain more fibrin, because the material for the nutrition of the body is derived from arterial blood, and the lymph and chyle, both of which contain fibrin in solution, are being constantly poured into the central parts of the circulating system. The result of several experiments instituted by Mayer and Berthold, was the same. I thought it necessary, however, to assure myself of the fact. I therefore extracted 1392 grains of blood from the jugular vein of a goat, and shortly afterwards 3004 grains from the carotid. The two kinds of blood were stirred separately so as to remove the fibrin, care being taken that none was lost. The arterial blood yielded $14\frac{1}{2}$ grains, the venous $5\frac{1}{2}$ grains of fibrin. So that in 100 parts of arterial blood there was 0·483, in the same quantity of venous blood 0·395 of fibrin. Denis gives the proportion of fibrin in arterial and venous blood as 25 to 24. Berthold found the proportion in the goat to be as 429 to 366, in the cat as 521 to 474, in the sheep as 566 to 475, and in the dog as 666 to 500.† The mean result of the foregoing experiments is that the quantities of the fibrin in arterial and venous blood are in the proportion of 29 to 24.

The substance which has been subjected to chemical analysis under the name of fibrin of the blood, is the matter which, while the blood is

* Lecanu, Transact. Med. 6 Oct. 1831. 92. † Burdach's Physiologie, iv. 282.

circulating, is in the state of solution, and coagulates when the blood is removed from the body: when obtained by stirring the blood, it is pure; but if procured by washing the coagulum, it may also contain the nuclei of the red particles. The proportion which these bodies form in it, cannot, however, be very great, for there is scarcely any difference in weight between the coagulum when deprived of its colouring matter by washing, and the fibrin obtained from the same quantity of blood by stirring. It is possible that the nuclei which in mammalia are so very minute, are removed with the colouring matter, and remain suspended in the solution; for by merely agitating the clot of the blood, whether of the frog or of mammalia, in the serum, a large number of the red particles can be separated in their perfect state from the coagulum, and float in the serum. And if the nuclei are really contained in the solution of colouring matter obtained by washing the crassamentum, they will be distinguished with difficulty even with the microscope; for if some water is added to a small quantity of blood under the microscope, the red colouring matter is dissolved, and neither the red particles nor their nuclei can then be distinctly seen; and if, in place of water, acetic acid is added, it is only by the most attentive observation that the small central bodies which remain after the solution of the colouring matter can be discerned. Whether the nuclei which I obtained from frog's blood consist of fibrin or not, is difficult to say; they have the more general properties of coagulated fibrin and albumen.*

Coagulation of inflammatory blood.—In inflammation, and under some other circumstances, the blood coagulates in an unusual manner. Before coagulation commences, the particles subside to a certain extent, leaving the upper part of the still fluid blood colourless or milky; and the upper layer of the gelatinous coagulum, which soon afterwards forms, is white or of a greyish yellow colour, while the lower part is red. During the contraction of the coagulum, these two portions of the clot diminish unequally in size; the upper whitish or greyish yellow substance contracts more firmly, and, although at first the coagulum occupied equally at all heights the entire diameter of the vessel which contains it, the whitish portion acquires at length a much smaller diameter than the red portion, and thus arises the peculiar form of the coagulum of inflamed blood. The cause of the unequal contraction of the two parts of the crassamentum is, that in the lower portion the fibrin is kept mechanically extended, as it were, by the red particles which it contains, while in the upper there are none of these bodies to prevent its close contraction. It must, however, be understood that fibrin is present and coagulates in all parts of the clot. The formation of a buffy coat may always be predicted before coagulation; for the subsidence of the red particles being a necessary condition, the surface of

* See page 120.

the blood is observed to become first transparent, and afterwards to acquire an opaline aspect. Mr. Hewson and Dr. B. Babington* have shown that the colourless fluid which produces this appearance can be removed with a spoon, and that it afterwards coagulates. This fact I have seen verified on the blood of a pregnant woman. [Dr. B. Babington removed sufficient of the colourless liquor sanguinis to obtain a clot from which the serum separated. He has observed that in shallow vessels the buffy coat is less perceptible for two reasons: first, that the blood coagulates in them more quickly than in deeper vessels; secondly, that the particles have less distance to subside. The form of the vessel also influences the size of the crassamentum, and therefore its proportion to the serum, which latter circumstance has been usually noted as important in disease. Thus the blood of the same person at the same bleeding, when drawn into a pear-shaped vessel, yielded a much smaller proportion of crassamentum than when drawn into a shallow basin; in the former case the proportion of the serum to the clot being as 1000 to 1292, in the latter as 1000 to 1717. In the former case, however, the clot is much more compact, the fibrin seeming to contract more firmly when its particles are less spread out and less distant from a common centre.†]

Cause of the buffy coat.—This peculiarity in the blood under certain circumstances, namely, the subsidence of the red particles to a certain extent before coagulation, might be supposed to depend on diminished specific gravity of the serum; but, for as much as is known, the serum of inflammatory blood has the same specific gravity as that of healthy blood. The fact that inflammatory blood coagulates more slowly than blood under ordinary circumstances, may in some measure explain the phenomenon, for it may be imagined that the red particles would thus have sufficient time to subside before the fibrin coagulates. This was the view that Hewson took of the formation of the buffy coat. To ascertain the correctness of this mode of explaining the phenomenon, I instituted a series of experiments with different kinds of blood. First, I wished to ascertain the time in which the red particles begin to subside in blood from which the fibrin had been removed. As I have mentioned already, this subsidence of the red particles in the serum takes place much more rapidly in the blood of cats and man than in that of sheep and oxen; in the former instances it amounts to one line in an hour and a half, and in several hours to from four to six lines. But this is not sufficient to explain the formation of the inflammatory crust; for although the coagulation of inflammatory blood takes place slowly, it does not occupy several hours, and, nevertheless, the buffy coat is frequently half an inch in thickness. I observed, in the next place, that the subsidence of the red particles is more rapid in blood of

* Medico-chirurgical Transact. vol. xvi. p. 11.

† Dr. Babington, loc. citat.

which the coagulation has been retarded by the addition of carbonate of potash; at least, in the case of the blood of man and that of the cat. This effect is not produced in the blood of sheep and oxen. In all the experiments in which the coagulation of healthy human blood was thus retarded, the red particles in five or six minutes sank one to two and a half lines below the surface, and within an hour as much as four or five lines. The supernatant fluid became gradually milky, and, if too much carbonate of potash had not been added, coagulated into a soft viscous fibrinous matter. In one case in which the blood was not inflammatory, the fibrinous coagulum became pretty firm, and formed a kind of buffy crust. With the blood of the cat I obtained the same result. Thus, by merely retarding the coagulation, I was able to give rise to the process by which the inflammatory crust is formed; the only difference being, that the fibrin which formed the artificial crust was softer and more glutinous; which depended, perhaps, on some chemical change effected by the carbonate of potash. There is another cause also for the greater firmness of the inflammatory crust; it is, that inflammatory blood contains more fibrin than healthy blood,—a fact which Sir C. Scudamore ascertained. It is difficult to say why the red particles should begin to subside in healthy blood as soon as it is drawn from the body, and yet sink so very slowly in blood deprived of its fibrin, even though it be inflammatory. The relative specific gravity of the serum and liquor sanguinis cannot be the cause, for the blood when deprived of its fibrin is specifically lighter than it was before. It may be that there is less adhesion exerted between the red particles and the liquor sanguinis, which still holds the fibrin in solution, than between the red particles and the serum without the fibrin.

Dr. J. Davy has observed, that inflammatory blood, in some instances, does not coagulate more slowly than healthy blood, and since the presence of fibrin in the blood appears from the above-mentioned experiments to favour the subsidence of the red particles, the formation of the buffy coat in these cases may arise from the blood containing a greater quantity of fibrin. So that the principal causes of the subsidence of the red particles and formation of the buffy coat in inflammatory blood appear to be the slow coagulation of the blood and the increased quantity of fibrin. The formation of a loose crust on the crassamentum in cases where we suspect a commencing disorganisation or decomposition of the blood, rather than that it contains an increased quantity of fibrin, is sufficiently explained by the slow coagulation of such blood.

Of the Serum.

The fluid which remains after the coagulation and contraction of the fibrin of the blood is called the serum, and, as we have before remarked, must not be confounded with the liquor sanguinis. It is yellowish, has

a saline taste, a specific gravity of 1·027 to 1·029, and, in the higher animals, has a distinct alkaline reaction. When exposed to a temperature of 158° or 167° Fahr., it is converted into a gelatinous mass by the coagulation of the albumen which it contains, and this takes place in vacuo as well as in atmospheric air. The albumen is its most essential component. Besides this, it contains a free alkali,—soda, (potash, also, according to Berzelius,)—combined with albumen and salts of these bases. We are indebted to Prevost and Dumas for the following table, showing the proportional quantity of the solid components of the serum and the other ingredients of the blood in different animals.

Name of Animal.	In 100 parts of Blood.			In 100 parts of Serum.	
	Coagulum.	Albumen.	Water.	Albumen.	Water.
Man	12·92	8·69	78·39	10·0	90·0
Simia callitriche	14·61	7·79	77·60	9·2	90·8
Dog	12·38	6·55	81·07	7·4	92·6
Cat	12·04	8·43	79·53	9·6	90·4
Horse	9·20	8·97	81·83	9·9	90·1
Calf	9·12	8·28	82·6	9·9	90·1
Sheep	9·35	7·72	82·93	8·5	91·5
Goat	10·20	8·34	81·46	9·3	90·7
Rabbit	9·38	6·83	83·79	10·9	89·1
Guinea-pig	12·80	8·72	78·48	10·0	90·0
Raven	14·66	5·64	79·70	6·6	93·4
Heron	13·26	5·92	80·82	6·8	93·2
Duck	15·01	8·47	76·52	9·9	90·1
Hen	15·71	6·30	77·99	7·5	92·5
Pigeon	17·57	4·69	79·74	5·5	94·5
Trout	6·38	7·25	86·37	7·7	92·3
Barbot	4·81	6·57	88·62	6·9	93·1
Eel	6·00	9·40	84·60	10·0	90·0
Tortoise	15·06	8·06	76·88	9·6	90·4
Frog	6·90	4·64	88·46	5·0	95·0

From this table it appears, that in the serum of human blood about one-tenth part in weight consists of solid ingredients in solution, the chief of which is albumen; and that this relative proportion is pretty nearly maintained even as low as the fishes: while in these animals,—the fishes,—and in the amphibia, the proportional quantity of the coagulum—fibrin and red particles—in the blood, is less than in the higher classes. The proportion of the solid parts of the crassamentum to those of the serum in human blood is as 12·92 to 8·69, or about 3 to 2. The blood of carnivorous animals yields more crassamentum than that of herbivorous animals. Dr. Davy states, that the blood of the lamb affords a softer and less abundant coagulum than the blood of the full-grown sheep. As Fourcroy has stated, the coagulum of fœtal blood also is, according to my observation, softer than that of the blood of the adult animal. From Berthold's* experiments it appears that the quantity of

* Beiträge zur Anat. Zool. ū Physiol. Gött. 1831.

fibrin in the blood of cold-blooded animals is as great as in that of warm-blooded animals, while the colouring matter is less in quantity.

Composition of the blood in the different sexes, ages, and temperaments.—This inquiry, and with it a new epoch in this department of Physiological Chemistry, was originated by Lecanu. Lecanu* seems to have made an extraordinary number of observations, and to have compared them with accuracy. He found the quantity of water in 1000 parts of blood to vary from 778·625 to 853·135, the average being 815·880. In the female it varies from 790·394 to 853·135; in the male, from 778·625 to 805·26. So that the blood of the female contains the greater proportion of water. This was the result also of Denis's experiments, of which twenty-four were made on men, and twenty-eight on women. The latter author found the proportion of water in man to vary from 805 to 732, in woman from 848 to 750. The mean proportion of the two is as 767 to 787. The quantity of water in the blood, according to Lecanu, bears no determined relation to the period of life; Denis, however, found its proportion greater in children and aged persons. With respect to the temperaments, Lecanu found that, in the sanguine temperament, the blood contains less water than it does in the lymphatic. In women of sanguine temperament, the proportion of water in four experiments varied from 790·394 to 796·175 in 1000 parts of blood; in women of phlegmatic temperament, it was found as the result of five experiments to vary from 790·840 to 827·130. The average in women of sanguine temperament was therefore 793·007; in those of the phlegmatic 803·710. From similar observations on men, the average for those of the sanguine temperament of this sex was found to be 786·584; for those of the phlegmatic 800·566. Thus, in the female sex, the excess of water in the phlegmatic temperament is 10·703; in the male it is 13·982.

The proportional quantity of albumen varies in general from 57·890 to 78·270; the quantity of albumen is nearly equal in the two sexes; it does not vary in any determinate degree between the ages of twenty and sixty, nor is there any striking difference in its quantity in the different temperaments.

The quantity of crassamentum in 1000 parts of blood varies generally from 68·349 to 148·450, the average being 108·399. In men it varies from 115·850 to 148·450, in women from 68·349 to 129·990; so that, according to Lecanu, the blood of men contains, in 1000 parts, about 32·980 parts more of the components of the crassamentum than the blood of women. The quantity of the coagulum does not, however, appear to increase proportionally with the age, at least not between the ages of 20 and 60 years. The quantity of the coagulum is, however, greater in the sanguine than in the phlegmatic temperament, which agrees with

* Beiträge zur Anat. Zool. ū Physiol. Gött. 1831.

Denis's observation. In four observations on women of sanguine temperaments the proportion of coagulum in 1000 parts of blood varied from 121·720 to 129·654; in five observations on women of phlegmatic temperament, from 92·670 to 129·990; the average in women of sanguine temperament being 126·174, in those of the phlegmatic 117·300,—the difference being 8·874. In men of the sanguine temperament the proportion of coagulum, in five observations, varied from 121·540 to 148·450; in those of the phlegmatic temperament, in two observations, it was 115·150 and 117·484. During menstruation Lecanu found that the blood contained less coagulum.

CHAPTER II.

CHEMICAL ANALYSIS OF THE BLOOD.*

1. *Of the Red Particles.*

The nuclei.—No complete chemical analysis of the nuclei of the red particles has hitherto been made, on account of the difficulty of obtaining these bodies in sufficient quantity. The red particles being large in frog's blood, the nuclei can be easily obtained free from their envelope by the method already described.† They are insoluble in water, and in acetic acid they remain several days without suffering any change; while they are soluble in a solution of alkali—of soda and potash, as well as of ammonia. In these characters they resemble coagulated fibrin and albumen, but the latter substances are more soluble in acetic acid. When the red particles of the frog's blood are treated with acetic acid, the nuclei are left in the form of a brown powder; fibrin and albumen, on the contrary, are rendered transparent by the action of this acid. But the brown colour of the nuclei probably depends, as I have before remarked, on their still retaining a portion of the colouring envelope, chemically changed by the acid; for nuclei previously freed from their red envelope by the action of water do not acquire this colour when acetic acid is added.

The colouring matter, hæmatin, cruorin.—Berzelius has analysed cruorin in three states:

1st. As it exists on the red particles; 2nd. dissolved in water; 3rd. in the coagulated state, in which it is insoluble in water.

1. The colouring matter in its natural state has a great affinity for oxygen, uniting with it, and becoming of a brighter colour whenever it comes into contact with it or atmospheric air. Carbonic acid is at the same time developed; this was the result of the experiments of Berthold, and of those of Christison and myself. If a stream of oxygen is passed through some blood from which the fibrin has been removed, this fluid becomes throughout of a bright red colour. The same change is effected

* In this chapter Berzelius is chiefly followed. † See page 104.

on the surface of blood thus prepared, as well as of freshly drawn blood, by mere exposure to air. By long contact with oxygen the colouring matter becomes black, (which arises, perhaps, from the carbonic acid formed having united with it,) and the bright red colour cannot then be again restored. Carbonic acid, sulphurous acid, and the acids generally, change the colour of the blood to a dark brown. Blood from which the fibrin has been removed absorbs nitrous oxide in large quantity, and becomes of a purple red colour; but its natural colour is restored by transmitting through it a stream of atmospheric air. Carburetted hydrogen is also said to communicate a brighter colour to dark blood. Several salts,—for example, common salt, nitre, and sulphate of soda,—have the same effect.* Schroeder Van der Kolk observed that bright red spots were produced on the surface of venous blood by the electric spark.

The colouring matter is dissolved by water in all proportions. It is obtained in the state of solution by washing the crassamentum; but as we cannot avoid removing the nuclei at the same time, these bodies suspended in the fluid necessarily enter into its analysis.

2. *The solution of the cruorin* is reddened less strongly than blood by exposure to air. By evaporating it at a temperature of 122° Fahr. a blackish mass is obtained which can be rubbed to a dark red powder, and is then again soluble in water. At 158° Fahr. the colouring matter in the watery solution coagulates, and is then insoluble. Alcohol and the mineral acids also coagulate it; and the addition of an alkali to its solution in acetic acid, or of an acid to its solution in an alkali, likewise precipitates it in a coagulated state. The precipitates thrown down by the salts of earths and metallic oxides are in part brown; others are black, and others red.†

3. *In the coagulated state* produced by a heat of 158° Fahr. the colouring matter is red and granular; when dried by heat, it becomes black. The long action of boiling water changes the red colouring matter, just as it does fibrin. Acids also form with coagulated cruorin, as with fibrin, neutral combinations, which are soluble in pure water; those formed with cruorin are of a dark brown colour. The coagulated cruorin is soluble in alkalies also. It is precipitated from its solutions in alkalies and acids by tannin. Tiedemann and Gmelin have discovered that it is slowly soluble in alcohol, giving this fluid a dark red colour. It may, therefore, be separated from the albumen which it contains, by means of alcohol, in which the albumen is insoluble. Lecanu, on this account, regarded the substance forming the pellicle of the red particles,—the hæmatosine,—as a compound of the true colouring matter which he calls globulin, and albumen. There is, however, no reason for this supposition; for the albumen may be derived from some serum, or from the nuclei of the red particles, separated with the colouring matter

* Berzelius, loc. cit. p. 48.

† Ib. pp. 50, 51.

from the clot during its ablution.* Michaelis gives the following as the result of his analysis of this substance:

	In Arterial Blood.	In Venous Blood.
Nitrogen, . . .	17·253	17·392
Carbon, . . .	51·382	53·231
Hydrogen, . . .	8·354	7·711
Oxygen, . . .	23·011	21·666
	100.	100.

From this it appears, that the elementary composition of the colouring matter agrees with that of fibrin: the former substance, however, leaves, when calcined, a larger quantity of ash; which ash contains a large proportion of iron; for Berzelius and Engelhardt have proved that Brande and Vauquelin were incorrect in asserting that the colouring matter does not contain a larger proportion of iron than the serum and other animal substances. Oehlenschläger† also discovered iron in the blood of puppies which had not yet sucked. Iron is therefore not an accidental ingredient derived from the food. The ash of the colouring matter is always alkaline, and of a red-brown colour; and, according to Berzelius, in human as well as in bullock's blood amounts to $1\frac{1}{4}$ or $1\frac{1}{3}$ per cent. of the weight of the dried colouring matter. In the colouring matter of calf's blood it amounts, according to Michaelis, to 2·2 per cent. Berzelius, in the analysis of 1·3 parts of ash, obtained from 100 parts of dried colouring matter, found

Carb. soda, with traces of phosph. soda, ...	0·3
Phosphate of lime, ...	0·1
Pure lime, ...	0·2
Subphosphate of iron, ...	0·1
Oxide of iron, ...	0·5
Carbonic acid, and loss, ...	0·1
	1·3

In another experiment Berzelius obtained from 400 grains of dried colouring matter, five grains of ash, which was composed of

Oxide of iron, ...	50·0
Subphosphate of iron, ...	7·5
Phosphate of lime, with a small quantity of phosp. magnes.	6·0
Pure lime, ...	20·0
Carbonic acid, and loss, ...	16·5
	100·0

The average result of Berzelius's experiments is, that the colouring matter contains rather more than one-half per cent. of its weight of metallic iron. Few persons have hitherto found manganese in the blood. In two grammes‡ of blood ashes, Wurzer§ found 0·108 of oxide of iron, and 0·034 oxide of manganese.

State in which iron exists in blood.—Menghini asserts that blood dried

* Lecanu in Poggendorf's Annal. 1832. iv. 550.

† Kastner's Archiv. 1831, Sept. Oct. p. 317.

‡ [A gramme equals 15·438 grains avoirdupois.] § Schweigger's Journ. lviii. p. 481.

and powdered is affected by the magnet, by virtue of the iron which it contains; while, according to Sir C. Scudamore, the red colouring matter, when calcined, is not so affected. None of the common and most delicate tests for oxide of iron,—as ferrocyanate of potash, tannin, gallic acid, and the strongest mineral acids,—detect the slightest traces of iron or phosphate of lime in the colouring matter before it is calcined; it appears, therefore, that the iron and lime of the blood are not in the state of salts. The assertion of Fourcroy, that the colouring matter is a solution of subphosphate of the peroxide of iron in albumen, and that the iron contained in the chyle is neutral phosphate of the protoxide of iron, is proved by the experiments of Berzelius to be incorrect; for the subphosphate of the peroxide of iron is insoluble in serum and in albumen, whether with or without the addition of an alkali. The opinion of MM. Prevost and Dumas, that the colouring matter is albumen containing peroxide of iron in solution, appears to be also incorrect; for the mineral acids and aqua regia should extract the iron from the uncalcined colouring matter* if such were its constitution.

Engelhart† has made some important discoveries relative to the share the iron has in producing the red colour. He first showed that a solution of colouring matter in water, when impregnated with sulphuretted hydrogen, after a time loses its colour, becoming first violet, then green. This is exactly the effect which the same gas has on iron; and the experiment therefore seems to prove that this metal contributes to the production of the red colour. Engelhart also found that all the iron, magnesium, and phosphorus, can be extracted from the watery solution of colouring matter, or from the coagulated colouring matter suspended in water, by passing a stream of chlorine through the fluid, or by mixing it with a solution of chlorine in water. The solution of colouring matter becomes at first greenish, and then quite colourless; the animal matter is precipitated in white flocculi combined with chlorine or hydrochloric acid; while the iron, calcium, magnesium, and phosphorus remain in the solution, combined either with oxygen or with chlorine,—the iron, for example, in the state of chloride of iron, the phosphorus as phosphoric acid,—and may be separated from it by filtration. The precipitated animal matter yields no ash by calcination. Now chlorine has no affinity for oxides, but has a very strong affinity for metals. Moreover iron is not extracted from the blood by muriatic and other mineral acids, although these acids have a great affinity for metallic oxides, but none for the metals themselves. Hence Berzelius considered it more probable that the iron in the blood is in the metallic state, not in the state of an oxide, although there is no analogous instance known of a quinary combination of a metal with nitrogen, carbon, hydrogen, and oxygen.

* Berzelius, loc. cit. p. 58. French translation, p. 61.

† De vera materiæ sanguini purpureum colorem impertientis natura. Göttingen, 1825.

M. Rose* has lately adduced new facts in support of the opinion, that the iron contained in the blood is in the condition of an oxide. Rose repeated Engelhart's experiment. By filtering the fluid after the change effected by the chlorine, and after the precipitation of the animal matter, the iron could be separated from the fluid; if, however, it were not filtered, but ammonia added in excess, all the precipitate was again dissolved and a dark red colour produced, and no iron was thrown down. Rose then mixed a solution of colouring matter with a certain quantity of persalt of iron, and added ammonia in excess, when the peroxide of iron remained in solution, and could be separated neither by sulphuretted hydrogen nor tincture of galls. Rose found, moreover, that when a persalt of iron is mixed in small quantity with a solution of many fixed organic substances, such as sugar, gum, starch, sugar of milk, and gelatine, the peroxide of iron cannot be precipitated from the fluid by alkalies. These experiments are certainly in favour of the supposition, that the iron in the colouring matter of the blood is in the state of an oxide combined with animal matter. Berzelius, however, is of opinion that the kind of combination which in the experiments of Rose retains the oxide of iron dissolved in the albumen or colouring matter, is not that by which it exists naturally in the colouring matter of the blood; because, were that the case, the iron would be extracted from the latter by acids, as it is from such artificial compounds of colouring matter or albumen with peroxide or protoxide of iron. When a mineral acid is added to such an artificial compound, the colouring matter or albumen is precipitated, and the oxide dissolved in the acid.

Berzelius believes, therefore, that the iron in the colouring matter is in the metallic state organically combined with nitrogen, carbon, hydrogen, and oxygen, together with a small quantity of phosphorus, calcium, and magnesium; and that by calcination of the colouring matter its elements are oxidised, so as to form phosphoric acid, lime, magnesia, and peroxide of iron. The state of the iron in the chyle seems also to favour this view; for in this fluid, in which the iron must be in quite a different state,—in the state of peroxide, namely,—Emmert† has found that it is extracted by nitric acid, and forms then with tincture of galls a black, with ferrocyanate of potash a blue, precipitate.

Meanwhile, Gmelin‡ opposes this view, which attributes the red colour of the blood principally to the iron, admitting even that iron in the metallic state be combined with nitrogen, carbon, oxygen, and hydrogen, in the colouring matter. He argues, that the discoloration of this substance when the iron is extracted, does not prove that the removal of the iron is the cause of the discoloration, for the bleaching action of the chlorine on the colouring matter may arise simply from its extracting the hydrogen so as to leave the oxygen to unite with its

* Poggendorf's Ann. vii. 81. † Reil's Archiv. 8. ‡ Gmelin's Chemie, iv. 1169.

other components, while the muriatic acid produced by the union of the chlorine and hydrogen might then dissolve the peroxide of iron of the alkaline fluid. When the serum mixed with colouring matter, says Gmelin, is treated with excess of cold muriatic or sulphuric acid, instead of with chlorine, and the colouring matter which is darkened, but by no means bleached, is separated by filtering, peroxide of iron can be discovered by means of sulphocyanate of potash in the serum, proving that the oxide of iron may be separated from the cruorin without the latter losing its colour. When blood from which the fibrin has been removed is evaporated, and the residue boiled repeatedly in alcohol, till very nearly deprived of its colour, this residue when calcined still yields a notable quantity of peroxide of iron.

Treviranus has offered a peculiar view of the condition of the iron in the blood. Winterl, by carbonising blood with potash, obtained a substance which was soluble in alcohol, and which did not, like ferro-prussiate of potash, precipitate iron from its combinations, but coloured it red. According to Treviranus, this substance, which Winterl called sanguineous acid (*blut säure*), is also contained in the saliva, and saliva becomes of a blood-red colour when mixed with a solution of iron in nitric or sulphuric acid. The colour produced when I repeated this experiment was, however, yellowish red, not blood-red. Treviranus supposes that the substance alluded to, combined with iron, is the cause of the red colour of the blood. Gmelin has discovered that in the saliva it is sulphocyanic acid that has this action on salts of iron. Kuehn, however, doubts this again.*

Hermbstaedt,† recently, from observing that sulphuretted hydrogen is developed during putrefaction in blood and albumen, as well as from several experiments, has been led to the conclusion that sulphur is an ingredient in the blood. The ash of calcined blood contains an alkali which must, Hermbstaedt concludes, be also contained in carbonised blood. If, however, carbonised blood be exposed to red heat with potash or soda, cyanuret of potassium or of sodium are formed. If cyanuret of potassium or sodium be heated to redness with sulphur, sulphocyanuret of potassium or sodium are produced, which have the property of imparting to the peroxide of iron a blood-red colour. In fact, serum, solution of albumen, or milk, if treated with sulphocyanic acid, become, says Hermbstaedt, of a blood-red colour, on adding a few drops of chloride of iron.

2. *The Fibrin.*

The fibrin has been examined hitherto only in the solid state; but by filtering fresh frog's blood, as I have directed at page 111, we obtain it in solution, and by allowing it as it passes through the paper to drop

* See the Analysis of the Saliva in the 2d book, chap. iv.

† Schweigger's Journ. 1832, v. and vi. p. 314.

into a watch-glass which contains acetic acid, its coagulation is prevented; or if, in place of acetic acid, the glass contains solution of common salt, the fibrin either does not coagulate at all, or only in a very small proportion. In the same way the coagulation of the fresh blood of the frog is delayed for a very long time, though not entirely prevented, by adding to it a solution of common salt. It has been long known that certain salts, such as sulphate of soda and nitrate of potash, when added in some quantity to fresh human blood, have the property of preventing its coagulation. And this in some measure explains the action of the cooling salts on the blood in the treatment of inflammation; they produce some change in the fibrin, which counteracts the great tendency that it has in inflammation to accumulate and coagulate in the vessels of the inflamed organ and on the surface of membranes after exudation.

It has also been long known that a watery solution of caustic potash or soda prevents the coagulation of human blood out of the body. According to MM. Prevost and Dumas, the coagulation of the blood of the higher animals, when removed from the body, is prevented by the addition of as little as $\frac{1}{1000}$th part of caustic potash. If the liquor sanguinis of the frog's blood, while filtering, is made to drop into a watch-glass in which there is some liquor potassæ, the fibrin does not coagulate to a clot, but there are slowly formed in it very small flocculi, which it requires close inspection to discover. The production of these flocculi is still more evident when the watch-glass contains sulphuric ether, fresh ether being added in proportion as it evaporates. No globules or flocculi are produced in the liquor sanguinis by the action of liquor ammoniæ.

Fresh coagulated fibrin may be obtained for chemical analysis by washing the coagula which adhere to the twigs with which fresh blood has been stirred, or by merely washing the crassamentum. As thus obtained, it is specifically heavier than water, serum, or blood deprived of its fibrin; it sinks in all these fluids if it is free from air-bubbles. The following description of fibrin is borrowed from Berzelius.

The coagulated fibrin when washed is white; by drying, it becomes yellowish, hard, and brittle, not transparent, and loses three-fourths of its weight. It softens again in water, but is not dissolved. It has no particular smell or taste. At the temperature at which it undergoes decomposition, it melts, puffs up, and burns, leaving a shining cinder, just as is the case with other substances which contain nitrogen. The cinder burns to a grey-white, compact, semi-fused ash, which amounts to $\frac{2}{3}$ per cent. of the weight of the dried fibrin. The ash is neither acid nor alkaline: after solution in muriatic acid it leaves traces of silica: it consists chiefly of phosphate of lime, some phosphate of magnesia, and a very slight trace of iron. The components of the ash cannot be extracted from the fibrin, before combustion, by acids, and appear there-

fore to have entered chemically into the composition of the fibrin, and not to have been merely mixed with it. In the coagulated state, fibrin is insoluble both in cold and warm water, but by long-continued boiling in water its composition undergoes a change; it shrivels up, becomes hard, and falls to pieces on the slightest pressure. During this change no gas is developed; but the fluid becomes turbid, and is afterwards found to contain a newly formed substance derived from the components of the fibrin. The solution of this new substance has no similarity to solution of gelatin.*

Fibrin, coagulated albumen, casein, and colouring matter of the blood have this character in common, that they yield no gelatin by boiling in water. Fibrin has also, with some other substances, (not albumen,) the property of decomposing peroxide of water by mere contact; oxygen being developed and water formed, while the fibrin remains unaltered. If the quantity of fibrin is large, heat is at the same time developed. With acids and alkalies it unites, playing in the one case the part of a base, in the other that of an acid, at least of an electro-negative substance. With concentrated acids it swells up, forming a transparent gelatinous acid substance; with diluted acids it forms a neutral compound, contracting considerably at the same time. The acid compound with the mineral acid is insoluble in water, the neutral compound is soluble; while both the neutral and acid compounds with acetic acid are soluble. The ferrocyanuret of potassium, when added to the solution of fibrin in acetic acid, throws down a precipitate, which is characteristic of fibrin; this not being the case with cellular tissue, tendinous structure, and the elastic tissue of arteries. Albumen is acted on by the acids in the same way as fibrin. According to Caventou and Bourdois, fibrin, albumen, casein, and mucus, are dissolved by cold concentrated muriatic acid, and if kept at a temperature of from 64° to 68° Fahr. acquire after twenty-four hours a beautiful blue colour; while this effect is not produced on gelatin and the substance of tendons. If the fibrin used in this experiment had not been perfectly freed from the colouring matter, the fluid, instead of being blue, was purple or violet. Fibrin, albumen, and casein, also agree in being dissolved to a gelatinous mass by caustic potash and soda, without being, like horn, converted into a soapy substance. The gaseous elements of fibrin according to the analysis of Gay-Lussac and Thenard, and that of Michaelis, are combined in the following proportions:

	Gay-Lussac and Thenard.	*Michaelis.* Arterial.	*Michaelis.* Venous.
Nitrogen	19·934	17·587	17·267
Carbon	53·360	51·374	50·440
Hydrogen	7·021	7·254	8·228
Oxygen	19·685	23·785	24·065†

* Berzelius, loc. cit. pp. 35, 36.

† See also Berzelius, loc. cit. pp. 34—47. E. H. Weber, loc. cit. p. 83.

Besides in the blood, fibrin also exists in solution in the chyle and lymph, and the muscles and uterus contain it in the solid state. In the fibres of the arteries, however, there is no fibrin.

3. *The Serum.*

If the coagulum formed by exposing serum to a temperature of 169° Fahr. be dried and then treated with boiling water, and the residuum left on evaporating the solution thus obtained be afterwards acted on repeatedly with alcohol, the alcohol will be found to take up lactate of soda, chloride of potassium and sodium, and osmazome; while the substance, which neither the boiling water nor alcohol dissolves, is pure albumen. The animal matters of the serum are, therefore, lactic acid, osmazome, and albumen.

All the components of the serum, with the exception of the albumen, are obtained in solution in a small quantity of water when freshly coagulated serum is subjected to a gentle pressure. The clear fluid which then exudes has been called "serosity." Besides the salts, $\frac{1}{50}$ of its weight is animal matter, which according to Brande is albumen, at least in part, it being coagulated by the action of galvanism. Dr. Bostock, however, maintains, that, if the serosity is in a pure state, it contains no albumen, but merely what Dr. Marcet and Thouvenet have called muco-extractive matter or osmazome.*]

(1.) *Lactic acid.*—This acid is composed of carbon, hydrogen, and oxygen; it has some analogy with acetic acid, but according to Berzelius is quite distinct from it. It forms with bases, salts of peculiar form, which Berzelius says are not produced by acetic acid rendered impure by animal matter. Pure lactic acid, prepared by the method most recently described by Berzelius, is colourless, without smell, and has a pungent acid taste, which is very quickly diminished by addition of water. It is soluble in alcohol in all proportions, while ether dissolves it in a small quantity only. It is found in muscle and in the crystalline lens, and, with its salts, occurs in many secretions, particularly in the milk. Lactic acid and its salts are always combined with osmazome, are extracted together with it by alcohol, but can be separated from it by means of infusion of galls, which precipitates the osmazome.

(2.) *Osmazome*, or animal extractive of Thouvenet, is soluble both in water and alcohol, whether they be hot or cold; it deliquesces in a damp atmosphere, melts in a warm air, and is precipitated from its solutions by infusion of galls. Osmazome is found by Gmelin to exist also in saliva, and in the pancreatic and gastric juices. Berzelius regards osmazome not as a peculiar substance, but as a compound of an animal matter with salts of lactic acid.

* Dr. Bostock's System of Physiology, p. 292.

(3.) *Albumen.*—The substance which remains after the extraction of the lactic acid and the osmazome from the dried coagulum of the serum is albumen. It is also an ingredient in lymph and chyle, in the white and yolk of the egg, (in the latter mixed with oil,) in the exhalations of the serous membranes, in the fluid of the cellular tissue, in the aqueous and vitreous humours of the eye, in the brain and nerves in combination with fat containing phosphorus, and in the contents of the Graafian vesicle of the ovary of mammalia and man. Here we have to consider principally the albumen of the serum, and this in two states.

a. Albumen in the state of solution.—In the serum it is in combination with soda, forming what is called albuminate of soda. Berzelius does not believe that the albumen of the serum is held in solution by means of the soda, for the soda may be saturated with acetic acid, without any precipitate being produced. Stromeyer found that ten drops of distilled vinegar are necessary to neutralise half an ounce of blood. If serum or solution of albumen be evaporated at a temperature below 140° Fahr. the albumen is left dry and transparent, and is in that state soluble in water. At a temperature between 158° and 167° Fahr. the albumen coagulates, and is then insoluble in water.

If serum be mixed with a large quantity of water, it no longer becomes solid by heat, but coagulates in globules, so as to form a milky fluid, which, however, when evaporated, yields coagulated albumen with the usual characters. Albumen is coagulated by the action of the galvanic battery, by alcohol, mineral acids, metallic salts,—for example, by salts of tin, lead, bismuth, silver, and mercury,—by chlorine, and by infusion of galls; and the same effect is produced on the albumen of the serum, according to the observations of Dutrochet and myself, by a very concentrated solution of fixed alkali,—for example, coagulation is produced when a small quantity of serum is mixed with a large quantity of liquor potassæ. White of egg, however, I find, is not coagulated by the liquor potassæ unless it (the white of egg) is in its undiluted state. Liquor potassæ precipitates also the albumen of lymph and chyle. Albumen of the egg is coagulated by pure ether, which produces no precipitate in serum. This was first observed by Gmelin, and I have since seen it confirmed.

My experiments on the fibrin in the fluid state as it exists in the blood have afforded me data for comparing it with albumen in a state of solution. Acetic acid produces no precipitate in serum, and none also in the solution of fibrin; thus the liquor sanguinis of frog's blood if allowed to drop from the filter into acetic acid does not coagulate. The neutral salts produce no precipitate in serum; and many of them —as the carbonates of potash and soda, nitrate of potash and sulphate of soda,—prevent the spontaneous coagulation of fibrin. Common salt has the same effect on the fibrin in frog's blood. Liquor ammoniæ

produces no precipitate in the fibrinous fluid obtained by filtration from frog's blood, any more than in solution of albumen or serum. Liquor potassæ precipitates the albumen from serum, and likewise precipitates in small flocculi the fibrin of the liquor sanguinis when this fluid is allowed to drop from the filter into a watch-glass containing liquor potassæ. Ether produces no precipitate in serum, but the fibrin coagulates when the liquor sanguinis of filtered frog's blood drops into a watch-glass containing ether. The coagulation of fibrin by liquor potassæ or ether differs from its spontaneous coagulation, inasmuch as in the latter case a completely coherent coagulum is formed which is at first transparent and gradually becomes turbid or opaque, while in the artificial coagulation the fibrin takes the form of separate globules, as is often the case with albumen when coagulated. The principal differences between the solution of fibrin and that of albumen in the serum, are, that the former coagulates spontaneously, while albumen coagulates only under the action of heat or certain reagents, and that the fibrin is precipitated by ether in the form of globules, while the albumen is not.

If albumen in solution is mixed with acids or alkalies, the part which unites with the reagent undergoes the same change as when it is coagulated, even although the reagent does not precipitate it; thus it is precipitated from the solution in acetic acid when potash is added, and from the alkaline solution on the addition of acids, just as is the case with colouring matter under similar circumstances.

If a small quantity of a metallic salt is mixed with serum, and a rather larger proportion of caustic potash added than is necessary for the decomposition of the metallic salt, the oxide is not precipitated, but remains in solution combined with the albumen. Berzelius, who mentions this, remarks that it is by this means that metallic salts, or oxides, are absorbed from the intestinal canal or the skin, carried into the circulation, dissolved in the serum, and expelled with the excretions; and hence it is that after the continued use of mercury we find the protoxide dissolved in the fluids of the body.* Would not the extremely intimate combinations of the metallic oxides with albumen be useful in medicine? Albumen or serum coagulates when mixed with concentrated solutions of earthy or metallic salts, and the coagulum contains the components of the salt. These coagulated combinations of albumen with salts also deserve a greater attention in medicine. Among the metallic salts already mentioned, the acetate of lead, and still more the bichloride of mercury, are remarkable as being the most delicate tests for albumen. Corrosive sublimate renders turbid a fluid which contains only $\frac{1}{2000}$th part of albumen in solution. From its great tendency to unite chemically with this salt, albumen is an antidote for it.

* Autenrieth and Zeller, Reil's Archiv. viii. Schubarth, Horn's Archiv. 1823, Nov. 417. Cantu, Mem. d. Tor. 29. 1825. Buchner's Toxicol. 538.

b. Albumen in the coagulated state, in which it consists of aggregated globules. In this state albumen has the same chemical properties as fibrin, and Berzelius knows no chemical test to distinguish them, except that coagulated albumen does not decompose the peroxide of water. Their elementary composition also differs little, as is seen by comparing the analyses of albumen given by Gay-Lussac and Thenard, Michaelis, and Prout, with those of fibrin given at page 127—

	Gay-Lussac and Thenard.	*Michaelis.* Arterial.	*Michaelis.* Venous.	*Prout.*
Nitrogen	15·705	15·562	15·505	15·550
Carbon	52·883	53·009	52·650	49·750
Hydrogen	7·540	6·993	7·359	8·775
Oxygen	23·872	24·436	24·484	26·925

Berzelius found the proportion of the albumen to the other components in 100 parts of the serum of human blood to be as follows:

Water		90·59
Albumen		8·00
Osmazome, with lactate of soda	Extracted by alcohol	0·40
Chloride of sodium	Extracted by alcohol	0·60
Modified albumen—alkaline, carbonate, and phosphate	Extracted by water	0·41
		100·00

In addition to these ingredients, Lecanu has found in the serum the sulphate of an alkali, carbonate and phosphate of magnesia, and phosphate of lime. Berzelius conjectures that the three principal components of the blood, fibrin, colouring matter, and albumen, are only modifications of one and the same substance; that the colouring matter, for example, may owe its peculiarity to the iron it contains. Treviranus is of the same opinion.

4. *Fatty matter of the blood.*

In some rare instances the blood contains fatty matter in a free state, which we then see floating on the surface; but the fatty matter of the blood is for the most part combined with the fibrin, colouring matter, and albumen. If the mixture of serum and red particles, obtained by stirring bullock's blood, be boiled with alcohol, and then filtered, the first portions of the fluid are found by Gmelin* to contain cholesterine, stearine, elaine, and stearic acid. Berzelius was formerly of opinion, that this fatty matter was formed during the chemical process. But it is most probable that fat is really contained in the fibrin, albumen, and colouring matter, and is merely extracted from it by the process of boiling in alcohol, for the chyle from which the blood is formed contains fatty matter in the free state, in the form of emulsion; and during the

* Chemie, iv. 1163.

formation of the blood this fatty matter unites probably more intimately with the other animal matters. Chevreul has by means of ether separated from fibrin a fatty matter, analogous to that which we obtain from the brain, and like that chiefly remarkable from containing phosphorus in a combined state. Berzelius also is now of opinion, that the fatty matter is only extracted, not produced, by the analysis; and he is led to this opinion more especially from observing that the fibrin is not chemically changed by the extraction of the fat by ether or alcohol, and that after the usual small quantity of fat is separated, no more can be obtained by continuing the process. The fatty matter of fibrin is, according to Berzelius, in a saponaceous state, for its solution in cold alcohol reddens litmus paper; a proof that at least a part of it must be in the state of an acid, as is the case after the process of conversion of a fat into soap. Berzelius describes two modifications of the fatty matter of fibrin, and concludes with the remark, that it has great resemblance to the acid salts of stearic and elaic acids with potash, described by Chevreul, except in its greater solubility in ether and alcohol. According to Chevreul, the fatty matter in fibrin amounts to 4 or $4\frac{1}{2}$ per cent. Lecanu found a crystallisable fatty matter, and an oily matter in the blood; of the first there were from 1·20 to 2·10 parts, of the latter from 1·00 to 1·30 parts in 1000 parts of serum. Boudet* confirms Gmelin's statement that the blood also contains cholesterine.

All kinds of fat are remarkable from the small quantity of oxygen, and the preponderating quantity of carbon, which enter into their composition. It is also remarkable that the fatty matters,—elaine and stearine,—which occur in the body in the free state, always combined one with the other, contain absolutely no nitrogen. Elaine and stearine are soluble in ether and hot alcohol, and the elaine remains dissolved in the alcohol even after it has cooled.

	Stearine.	Elaine.
Oxygen	9·454	9·548
Hydrogen	11·770	11·422
Carbon	78·776	79·030

Other fatty matters,—for instance, that of the blood,—are combined with other animal substances, they crystallise in part when exposed to the cold, contain nitrogen, and cannot be converted into soap. The fatty matters of the blood and brain contain phosphorus also. Fatty matters of this kind occur in a combined state in the blood, cerebral and nervous substance, in the liver, and perhaps in some other parts.

If the new organic matters formed by the secretions,—such as picromel, casein, mucus, &c.—are not taken into consideration, the blood will be found to contain the proximate elements of all the solid parts of the body,—namely, fibrin, albumen, osmazome, lactic acid, and

* Essai Critique et Experimental sur le Sang. Paris, 1833.

fatty matter. The only exception is the gelatin or gluten which is obtained from the tendinous fibres, cartilages, bones, serous membranes, and from the cellular tissue generally, particularly from the cellular tissue of the muscles. Parmentier and Deyeux, and Saissy thought, indeed, that they had discovered gelatin also in the blood. But this was evidently an error. It is a question, however, whether gelatin generally is not formed during the changes produced in the composition of the tissues by boiling. Gelatin is obtained from the parts mentioned by boiling water: it is insoluble in alcohol and cold water, by which it is distinguished from osmazome: it forms a jelly on cooling even when dissolved in one hundred and fifty times its weight of water: in this jelly it is combined with water, and is again soluble in boiling water, by which it is distinguished from fibrin and albumen. It is slowly soluble in acids and alkalies, and is precipitated by tannin and chlorine. E. H. Weber has stated several facts which render it probable that gelatin does not originally exist in the body, but is formed by the decomposition of other animal matters, in which opinion Berzelius, Prochaska, and Ficinius concur. The strongest argument in favour of this opinion is, that, according to the statement of Berthollet, flesh of animals, which by boiling in water has ceased to afford gelatin, reacquires that property after undergoing putrefaction in a close air with developement of carbonic acid.*

CHAPTER III.

ANALYSIS OF THE BLOOD BY GALVANISM.†

Dutrochet has made some ingenious experiments respecting the action of galvanism on animal substances. He even flattered himself that he had formed muscular fibres from albumen by the agency of galvanism, and supposed that the red particles of the blood formed each a pair of plates, the nucleus being negative, the envelope positive. But all the appearances which he has attributed to different electric properties of the blood are explicable by the precipitation of the albumen and fibrin in consequence of the decomposition of the salts of the serum, and of the oxidation of the copper wire used in the experiments—both the decomposition of the salts and the oxidation of the copper being the usual effects of galvanic action.‡

* Consult Wienholt. Meckel's Archiv. i. p. 206. Berzelius, loc. cit. p. 661. The French translation, p. 703.

† The original observations are in Poggendorf's Annal. 1832, 8.

‡ [The translator has conceived it to be better to place the long detail of experiments, which the author enters into for the purpose of refuting Dutrochet's erroneous views, in the form of a note, giving in the text merely the inference that he deduces from the experiments.]

If a drop of a watery solution of yolk of egg (in which very minute microscopic globules are suspended) be submitted to the action of galvanism, we soon remark the

Should any physiologist be so fortunate as to prove beyond doubt the electric property of the blood, I could only congratulate science on the great advance which it would thus have made. Till then it is proper to submit to severe criticism all experiments which do not justify the con-

waves (ondes) which were first observed by Dutrochet (Ann. d. Sc. Nat. 1831). The wave originating at the copper or negative pole, is transparent on account of the albumen being dissolved by the alkali; while that commencing at the positive or zinc pole where the acid collects, is opaque and whitish, particularly near the wire. The two waves tend towards each other, and at the moment of contact a linear coagulum is suddenly formed along the line at which the two waves meet, and has therefore exactly the form of that line; it is waving like the border of the two undulations at the moment of their meeting. A visible movement attends the formation of the coagulum; as soon, however, as it is formed, all is still, and not the slightest movement is afterwards perceptible. It is therefore difficult to conceive how an observer of the first rank, like Dutrochet, could pronounce this coagulum of albumen to be a contractile muscular fibre produced by electricity. It is nothing more than coagulated albumen, and is quite soft, like the albumen which collects around the zinc wire in galvanising serum. It consists of globules which can be easily wiped asunder, and which have been merely deposited in the form of the line of contact of the two currents without any cohesion. If both wires are placed in a drop of serum, whether of the blood of the frog or of one of the mammalia, no distinct waves are perceptible; but a deposition of globules of albumen takes place at the zinc wire, and gradually increases, the globules first deposited around the wire being pressed outwards, while a new deposition takes place. According to the view which Dutrochet takes of the action of galvanism on animal substances, we must consider the albumen of the serum as a negative electric body, since it is deposited at the zinc or positive pole of the battery. But the real cause of its precipitation is the coagulation of the albumen by the acid which is derived from the decomposition of the salts, and collected at the positive pole. The albumen is not deposited around the negative wire, because it is there held in solution by the alkali. By a very powerful battery, however, the albumen is precipitated at the copper wire also, as Gmelin has pointed out: this depends either upon the heat developed, or, what is more probable, on the circumstance of a concentrated solution of a fixed alkali, having the power of precipitating albumen, a fact observed both by Dutrochet and myself. The difference of the quantity of the salts in the two fluids clearly explains why with a battery of the same strength albumen is copiously precipitated around the zinc or positive wire in the serum, while in solution of yolk of egg merely a turbid undulation is perceived, and no coagulum is found until this undulation meets that from the negative pole. Lassaigne (Ann. d. Chim. et d. Phys. t. xx. p. 97. Weber's Anat. t. i. p. 87.) coagulated albumen by alcohol, then washed it with the same fluid until chloride of soda could be no longer detected in it by means of nitrate of silver. Of the coagulum thus free from salts, water took up $\frac{7}{1000}$, and the small quantity of albumen thus dissolved did not coagulate under the influence of galvanism, because it contained no muriate of soda: it coagulated when this salt was added.

Were I to explain the above experiments on Dutrochet's principles, the albumen of the yolk of egg would be neutral, for it does not coagulate till the two currents meet, whereas the albumen of the serum would be negative electric, for it coagulates at the positive pole. But we need only add to the solution of the yolk of egg some common salt, and it coagulates at the positive pole, and no currents are formed. If we expose to the action of a galvanic pile a drop of the blood of a frog, or of a mammiferous animal,

clusions deduced from them: the conclusions being but too readily admitted by those who do not repeat the experiments.

I have already mentioned that with the galvanometer no electric current can be discovered in the blood; I perceived no variation of the

spread thinly out, the usual gaseous bubbles are formed around the copper wire, and around the zinc wire the albumen coagulates to a soft mass of granules, just as when serum is treated in the same manner. The red particles, on the contrary, do not collect either at the positive or at the negative pole. The coagulation of the fibrin is neither accelerated nor retarded; it takes place neither around the positive nor the negative pole particularly, but throughout the entire drop between the two wires, and in the circumference of the fluid at some distance from them. Immediately around the wires the red particles are decomposed by the acid and alkali collecting there. In the other parts of the drop they suffer no change. The coagulation of the fibrin takes place in the same way when arterial or venous blood of the rabbit is used instead of frog's blood.

When a drop of frog's blood from which the fibrin has been removed, is exposed to the action of galvanism, it presents the same phenomena as fresh blood, with the exception of those dependent on the presence of fibrin. If a drop of the strongest possible solution of colouring matter, obtained by washing the crassamentum of the blood of quadrupeds which has been previously freed as completely as is possible from the serum it contains by means of blotting paper, was subjected to the voltaic pile, I obtained different results according as I closed the circle with the copper wire itself, or fixed a piece of platinum wire on the extremity of it, so that the quick oxidation of the copper might not interfere with the experiment. In the last case the results were the same as those described by Dutrochet; in the first case they were different. When I used a bare copper wire to close the circle, a red pulpy coagulum of albumen and colouring matter formed around the zinc wire. The coagulum gradually increased by new depositions around the zinc wire, extending the original red ring. The later depositions were, however, less red than the first—mostly of a whitish grey colour. The coagulation takes place all around the zinc wire, but extends rather further in the direction of the copper wire than in other directions. The precipitate has the form of the wave in the preceding experiments, but is formed of a consistent pulp. At the copper wire the usual developement of gas is remarked, and sometimes a very indistinct undulation, in which the colouring matter remains dissolved, as in the rest of the fluid: the border of this undulation is of a somewhat deeper red than the rest of the fluid. Dutrochet calls this a red wave, but for this there is no reason. The alkali which collects around the negative wire usually holds in solution the animal matter of the fluid, which, in this case, contains red colouring matter in solution, as does the rest of the fluid, while around the positive pole the albumen and colouring matter coagulate. The description which Dutrochet gives of the effects of galvanism on the solution of colouring matter is quite different. (See Froriep's Notiz. No. 715.) Thus, he says, that two undulations appear; the one at the zinc pole was acid and transparent, and, as it increased, drove before it the colouring matter, which collected in the upper part of the fluid around and beyond it; the alkaline wave at the copper pole was on the contrary occupied by the colouring matter. The two waves formed in uniting a slight coagulum derived from the albumen of the serum removed from the crassamentum with the colouring matter. The red colouring matter combined almost wholly with this coagulum. From this experiment, in which the red colouring matter is said to retire from the positive pole and collect at the negative pole, Dutrochet without reason concludes that this substance is an electro-positive body. I have already stated that

magnetic needle of the multiplicator, even when I inserted one wire into an artery of a living animal, the other into a vein. Bellingeri believed that he had discovered a means of proving the electric property of the blood by the contractions excited in the leg of a frog, when

when I used copper wire to close the circle, the colouring matter coagulated with the albumen around the zinc pole, and the red coagulum by further coagulation of the albumen was only further extended. If, however, I put a piece of an unoxidisable metal, as platinum, on the end of the copper wire, to avoid the influence of the oxidation of the latter, the appearances were exactly those described by Dutrochet. There were now really formed at the copper and zinc poles two waves which tended towards each other, each wave having a distinct red border. Dutrochet overlooked the red border in the wave of the copper pole. The wave of the copper pole is not redder than the rest of the fluid ; it is its border only which is redder. Dutrochet is therefore incorrect when he says, the colouring matter accumulates at the copper pole. I have repeated the experiment very often, and have never seen this accumulation take place. The red colouring matter in the red border of the wave of the copper pole retires, indeed, in some measure from the copper wire, as that in the border of the wave of the positive pole does from the zinc wave. Although the undulation from the negative pole is not redder than the rest of the drop, that of the positive pole, on the contrary, is in fact less coloured than the fluid beyond the wave, but yet not quite colourless. The border of the more transparent wave of the positive pole is redder than that of the wave of the negative or copper pole, which is, however, itself remarkable from its deeper colour : in the border of the wave of the copper pole the colouring matter is in the state of a concentrated solution ; in the margin of the wave of the zinc pole the colouring matter is in the form of very small globules. This experiment appears to me to be very similar to that in which solution of yolk of egg is exposed to the action of the voltaic pile. If in the experiment on the solution of colouring matter bare copper wire is used to close the circle, the colouring matter and albumen coagulate at the zinc pole. If common salt be added to the solution of yolk of egg, the albumen coagulates at the zinc pole. If common salt is mixed with solution of colouring matter, it is acted on, even with the platinum wire, like the solution of yolk of egg with common salt ; no waves are formed, and a whitish coagulum collects at the zinc pole. All these facts being considered, Dutrochet's assertion that the colouring matter of the blood is electro-positive, appears to me unfounded.

Dutrochet having obtained some fibrin free from colouring matter, by washing the crassamentum, which he incorrectly regards as formed by the aggregation of the nuclei of the red particles, dissolved it in a weak alkaline solution, and then subjected it to the action of a voltaic pile : hydrogen was developed in considerable quantity at the negative pole ; at the positive, oxygen ; but at neither was any undulation formed : the fibrin coagulated at the positive pole only ; whence Dutrochet concludes that the alkaline solution of fibrin is acted on as a neutral salt, of which the alkali passes over to the negative pole, and the acid to the positive, and therefore that the fibrin is a negative electric substance. We know, however, that fibrin can unite both with acids and alkalies ; in the one case acting the part of a base, in the other that of an acid. From its forming neutral compounds with mineral acids, we might have come to a conclusion the very opposite of that of Dutrochet. However, in repeating Dutrochet's experiments, as might be expected from so exact an observer, I found them in most points correct. When I exposed a solution of fibrin of the blood in a weak alkali, on a glass plate or in a watch-glass, to the action of the voltaic pile, a white pulpy coagulum was deposited in small quantity at the positive pole. I had washed the fibrin, obtained by stirring bullock's blood for a

a circle, formed of blood, the nerve and muscle of the limb, and a metal, is closed by bringing the blood and metal in contact. He set out from the principle, that by contact of two heterogeneous bodies the electricity present in them is thrown into a state of greater or less tension, and

long time on the filter, so that I could be pretty sure that it was free from serum and the salts of serum: it appears therefore, at first view, that the alkaline solution of fibrin does really separate into electro-negative fibrin and electro-positive alkali. In coming to this conclusion, however, the mineral substances and salts which are ingredients in the fibrin itself are lost sight of; their decomposition by the galvanic pile would necessarily be attended by the developement of acid at the positive pole, and therefore might cause the fibrin to coagulate by forming with it a neutral substance. However, there are still objections which may be urged against the value of the experiment itself. The effect described by Dutrochet only occurs when copper wires are used. I never observed it, though I made the experiment repeatedly, when, to prevent the oxidation of the end of the copper wire of the zinc pole, a piece of platinum wire had been affixed to the end of it. Dutrochet seems to have made his experiments merely with copper wires. If platinum wire is used at the positive pole, the developement of gas remains the same; indeed, still more gas than before is formed at the positive pole, because it no longer oxidises the copper wire as before. But not the slightest trace of a coagulum is formed at the zinc pole or around the platinum wire. Hence we must conclude that the formation of a coagulum from an alkaline solution of fibrin, at the positive pole, when the copper wire is used, is dependent on the oxidation of the copper.

It appears then that the alkaline solution of fibrin is not decomposed by the galvanic pile, unless copper wire, which so readily suffers oxidation, is employed at the zinc pole; and therefore that fibrin is not proved to have the character of an electro-negative body. How much the precipitation of the albumen and fibrin depends on the salts contained in the solution, is shown by the following circumstances:—Alkaline solution of fibrin never deposits the slightest coagulum around the platinum wire of the zinc pole; but this coagulation takes place immediately that some common salt is added to the solution, the muriatic acid of the salt in that case causing the coagulation at the zinc pole: consequently, before making experiments with galvanism on a solution of fibrin in a weak alkali, the fibrin must be completely free from serum, for serum contains muriate of soda. We may obtain it thus pure by washing the coagulum, obtained by stirring blood, for a long time with a large quantity of water.

It occurred to me that it would be very interesting to try the action of the galvanic pile on the still fluid fibrin of the liquor sanguinis. For this purpose, equal quantities of distilled water and frog's blood were poured into the filter (as described at page 111), and the fluid which passed through was immediately subjected to the wires of the galvanic pile. At the zinc pole a pulpy coagulum of albumen was immediately formed. The transparent fibrin collected at neither pole, but coagulated in the middle of the fluid in the watch-glass, in the form of an isolated clot, quite unaffected by the action of the galvanic apparatus. It coagulated in the usual time. The albuminous deposit at the zinc pole was of the same kind as I had obtained it by application of the galvanic pile to blood freed from the coagula of fibrin.

I have also tried the action of the voltaic pile on the colourless nuclei of the red particles of the frog's blood. The red particles were freed from their coating of colouring matter, as already described, by means of a large quantity of water. The greatest part of the supernatant fluid was taken up again with a syphon, and the white sediment being then mixed with some water, a drop spread upon a glass plate was subjected to the action of galvanism. The same phenomena were produced as when a watery

that this tension is so much the greater the more distant these bodies are one from the other in a scale in which they are arranged according to their electrical properties. Bellingeri arranged the metals in the following order:—zinc, lead, mercury, antimony, iron, copper, bismuth, gold, platinum. He compared the electrical property of the blood with that of the above-mentioned metals, blood being brought into contact with one of the metals, and the blood and metal with the nerve and leg of the frog, when the contraction of the frog's leg served as electrometer. He had found, he says, that when two metals are brought into contact, respectively with the nerve and muscle of a frog which had already lost some portion of its irritability, that metal is positive with regard to the other, which when applied to the muscle excites contraction at the moment that the circle is closed, and either not at all, or only at the moment of interrupting the circle, when applied to the nerve. (The reverse, however, is the fact.) M. Bellingeri asserts, that when he tested the electric property of the blood in this way, substituting it for one of the metals, he found that it stands in different relations to different metals, and that in general it evidenced the same electric property in relation to the other metals as iron. Arterial and venous blood did not differ in this respect. The electric property of the blood is preserved, he says, long after its abstraction from the vessels.* It is inconceivable how any great value can be accorded to these experiments. I have already recounted the experiments which I made on the frog in the spring before the breeding season of the animal; when by laying the nerve of the frog's leg in a small saucer containing blood or water, (it was indifferent which,) and bringing the muscles of the leg and the blood in contact by means of a piece of copper wire, a contraction in the leg of the frog was produced. In repeating this experiment now in the cold season of autumn (end of October), I obtain the same results, and am convinced that the rare electric phenomena already related† are

solution of yolk of egg is exposed to the same influence: two waves were formed; that of the zinc pole was turbid and drove before it the minute globules, that of the copper pole was transparent and contained no globules. When the experiment was made with solution of colouring matter, the wave arising at the zinc pole drove before it red globules, while in this mixture of nuclei of the red particles with water, the particles at the margin of the same wave were white. This experiment shows that there is no electric difference between the nucleus and its envelope. The only apparent difference was, that the wave at the zinc pole in the solution of colouring matter was more transparent, while in the mixture of nuclei of the red corpuscules and water, as in the solution of yolk of egg, which also contains globules, it was turbid.

While I differ from Dutrochet in many points in the results of my observations, I must express my admiration of the ingenuity displayed by this talented inquirer in endeavouring to solve this difficult question.

* Froriep's Notiz. 408. See also page 73 of this work. † Page 69.

produced, not merely before the time of pairing in the spring, but also with the same facility in the cold autumn season. In this experiment it is evident, that a circle of copper and water between the nerve and muscle is perfectly as efficient as one of copper and blood. What then has Bellingeri proved if the electric quality of water is the same as that of blood? It is, indeed, very probable, that neither the blood nor the water excites the electricity in this circle; they may be mere conductors, the electricity being developed between the copper and the muscle.

CHAPTER IV.

OF THE ORGANIC PROPERTIES AND RELATIONS OF THE BLOOD.

a. The vivifying influence of the blood.

The arterial blood in its course through the capillary vessels of the body loses its bright red colour and becomes again venous. The unknown reciprocal action between the blood and the organised matter, by which this change is effected, maintains the vitality of the organs, at the same time that it renders the blood incapable of again exercising this necessary vital stimulus until it has regained its arterial character in the lungs. In the process of arterialisation, the blood absorbs oxygen from the atmosphere and gives out carbonic acid,—the oxygen which it absorbs being in greater quantity than the carbonic acid exhaled. The same portion of blood acquires and again loses its arterial properties within the period of a few minutes; for it will be shown at a future page, that the blood circulates through the whole body in that space of time. It is only while in its arterial state that the blood is capable of maintaining life. The suppression of the change which the blood undergoes in the lungs produces asphyxia and death, chiefly, as Bichat has shown, by interrupting the functions of the brain and nervous system. The necessity for arterial blood is less urgent, however, in new-born children, and still less so during the state of hybernation and torpor, and in the lower animals; in the fœtus of the mammalia the necessity for the aeration of the blood seems to be wholly wanting. The functions most dependent on the arterial state of the blood are those of the nervous system, and those of animal life generally. This is evidenced by the symptoms of the morbus cœruleus, in which the two kinds of blood continue, from some defect in the circulating organs,—for instance, a persistence of the canal in the ductus arteriosus, or of the foramen ovale,—to be partly mixed. Nutrition and secretion are here little interfered with, even although the surface is dusky and blueish: but the muscular power fails; the slightest exertions bring on symptoms of suffocation, fainting, and even asphyxia; the sexual passion is not developed,

the temperature is lower than natural, and there is a tendency to hemorrhage even to a fatal extent.* That arterial blood is not so necessary for the performance of the functions of organic life is moreover deducible from the fact, that secretions are in some cases formed by organs which receive a much larger quantity of venous than of arterial blood. Thus the bile is secreted in part from the venous blood of the porta, the urine in reptiles and fishes in greater part from the venous blood which in these animals is carried to the kidneys by afferent veins which are independent of the arteries, and of the efferent veins that return the blood to the heart.

The application of a ligature to all the arterial trunks of a limb deprives it of power of motion, and at last of vitality. Great losses of blood produce immediate asphyxia in the higher animals: cold-blooded animals, however, survive for a considerable time the abstraction of the greater part of their blood, and frogs live many hours even after the removal of the heart, and retain perfect power of motion. But even parts which have been removed from the body, and have lost their irritability, appear to recover in some degree their vitality by immersion in blood, as in the case of the heart of the frog in Von Humboldt's experiments.

Transfusion of blood.—Prevost and Dumas showed that the vivifying power of the blood does not reside so much in the serum as in the red particles. An animal bled to syncope, is not revived by the injection of water or pure serum of a temperature of 68° Fahr. into its vessels. But if blood of one of the same species is used, the animal seems to acquire fresh life at every stroke of the piston, and is at last restored. Professor Dieffenbach has confirmed these experiments. It is stated by Prevost and Dumas, and by Dieffenbach, that revival takes place likewise when the blood injected has been previously deprived of its fibrin. I have shown that the red particles of the blood remain perfectly unchanged after the removal of the fibrin; blood, therefore, from which the fibrin has been removed, and heated to the proper temperature, ought to be preferred in the few cases where transfusion of blood is justifiable, or necessary, on account of hemorrhage; for in this state the blood is completely fluid and remains so, and thus the principal difficulty of transfusion, namely, the ready coagulation of the blood in passing from one animal to the other, is avoided. Blood of animals of a different genus, of which the corpuscules, though of the same form, have a different size, effect an imperfect restoration, and the animal generally dies in six days. The pulse becomes quicker, the breathing remains natural, but the temperature sinks very rapidly; the excretions are mucous and

* Consult Nasse's Remarks on the influence of arterial blood on the developement and functions of the human body, founded on cases of the morbus cœruleus. Reil's Archiv. t. x. p. 213.

bloody; the cerebral functions seem to be unaffected. The same symptoms ensue when the serum and red particles without the fibrin are injected.

The injection of blood with circular corpuscules into the vessels of a bird (in which the corpuscules are elliptic and of larger size), produces violent symptoms similar to those of the strongest poisons, and generally death, which ensues, indeed, instantaneously, even when a small quantity only of the blood has been injected; such, for example, was the effect of the transfusion of some blood of the sheep into the veins of a duck; while in many cases in which the blood of sheep and oxen was injected into the vessels of cats and rabbits, these animals were revived for a few days. The fact of the blood of mammalia being poisonous to birds is very remarkable; it cannot be explained mechanically. The injection of fluids containing globules of greater diameter than the capillary vessels produces death by obstructing the pulmonary vessels, and producing asphyxia; but the corpuscules of the blood in mammalia are even smaller than those of birds. In Dieffenbach's* numerous experiments, pigeons were killed by a few drops only of the blood of mammalia. The blood of fishes is said to be fatal to mammalia as well as to birds.

[The interesting experiments of Dr. Bischoff † throw new light on the subject of transfusion. He confirms the statements of Prevost and Dumas, and of Dieffenbach, as to the deadly effect of the blood of mammalia injected into the veins of birds. In all his experiments made with the fresh blood of mammalia, the birds (common fowls) died within a few seconds after the performance of the transfusion, with violent symptoms resembling those of poisoning. But when, instead of the fresh unchanged blood, he injected blood from which the fibrin had been removed by stirring, and which was heated to the proper temperature, he was surprised to find that no symptoms were produced,—the animal appeared to suffer no inconvenience. These experiments were performed repeatedly, so that there could be no fallacy in the result. I was present when Dr. Bischoff performed them before his class at Heidelberg in July 1835. The deadly effect then of the blood of mammalia on birds is in some way connected with the fibrin of the blood. The principle which renders the blood of one class of animals thus injurious for another class, is not, Dr. Bischoff remarks, identical with the vivifying principle of the blood, which might be supposed to be peculiar to each individual class, and deadly to others; for the blood, when thus deprived of its fibrin, has still the effect of perfectly restoring the animal from which it was taken, although the latter be reduced by loss of blood to extreme syncope or apparent death: but it is an important fact, that

* Die Transfusion des Blutes, von Dieffenbach. Berlin, 1828.

† Müller's Archiv. 1835.

when blood thus deprived of its fibrin is injected into the veins of an animal of a different class, reduced to a similar state of syncope, no revival takes place,—the animal dies. Hence the blood of an animal of a different class, even when deprived of its fibrin, although not poisonous, is not adapted for the operation of transfusion, in cases where this is necessary in man.

Dr. Bischoff mentions but one experiment in which he injected the blood of a hen (about half an ounce), deprived of its fibrin and warmed, into the vessels of a dog, and in this instance no other effect was produced on the animal than a state of exhaustion which might be the result of his struggles during the operation.

The experiments of Dr. Bischoff on the transfusion of different kinds of blood into the veins of frogs, are from the difficulty of the operation less satisfactory. The results, however, which he has deduced from them seem to be tolerably certain. The blood he used was in all cases deprived of its fibrin, and its effects so far corresponded with those on the higher classes of vertebrata that it did not produce an immediately fatal result; but it nevertheless had a marked injurious effect on the system, and this was most violent when human blood was injected, less so when that of mammalia and birds was used. The blood of fishes had in several instances no particular effect. When the blood of crabs was injected, the frogs lived several days, but died eventually. The effect of the transfusion of the blood of man, mammalia, and birds, was always death, generally in a few hours, the only symptom being diminished activity of the circulating organs; the heart in some cases seemed to be paralysed. After death there was found in almost all cases effusions of a reddish serum, containing the red particles of the frog mixed with those of the blood injected, particularly in the stomach and abdominal cavity.]

An incautious injection of air into the veins and blood of a living animal is almost immediately fatal by obstructing the circulation in the small vessels, and in the heart. Nevertheless, in Nysten's experiments, very small quantities, not only of atmospheric air and oxygen, but even of irrespirable gases, such as nitrogen, nitrous oxide, hydrogen, carburetted hydrogen, carbonic acid, and carbonic oxide, were injected into the vessels without fatal consequences. Nitric oxide gas, sulphuretted hydrogen, ammonia, and chlorine, were the only gases which he found to be deadly.*

b. Evidences of life in the blood itself.

Automatic motions of the blood-corpuscules.—Professor C. H. Schultz has spoken of an active vital process which can be seen to be constantly going on between the individual molecules of the blood and the sub-

* Nysten, Recherches de Physiol. et de Chim. Pathol. Paris, 1811.

stance of the vessels.* When the circulation of the blood is observed in transparent parts viewed by bright daylight, (not by the direct rays of the sun, which produce a dazzling but very confused illumination from being refracted by the transparent animal structures,) there is not the slightest appearance of spontaneous independent motion of the individual red particles. During the last ten years I have examined the circulation of the blood in the most various parts, at every opportunity, and with different instruments; but have never, when the object was well illuminated, seen what Schultz describes,—I mean the constant assimilation, disappearance, and new formation of the globules; nor have other observers—Rudolphi, Purkinje, Koch, and Meyen,—been more successful than I have been. The observer may convince himself also that the motion of the red particles in the circulation is passive, by compressing the vessels of a limb, or the whole limb itself. Neither under these circumstances, nor at other times, do the globules show any attraction or reciprocal action among themselves. If, however, the direct rays of the sun are allowed to shine through a transparent part, the distinctness of the image is entirely lost owing to the refraction of light which is produced by the inequalities of the surface, as well as by the red particles which act as so many little lenses; the observer no longer perceives the red particles flowing through the vessels, but there is a general sparkling flickering motion, in which frequently even the direction of the current is not distinguishable. The same deception of vision is produced, when a fluid containing globules—milk, for example—is viewed while flowing over the surface of a glass under the microscope, by the direct rays of the sun; and even clear water flowing over the surface of ground glass has by a similar light the same appearance.†

The notion of Eber and Mayer,‡ that the red particles are infusory animals, is still less admissible. The theory which ascribes to the blood a self-propelling power—a power of motion, which continues when the heart has ceased to act—will be considered in treating of circulation in the capillaries. §

Treviranus, Mayer, and others, have regarded as an automatic movement that confused motion of the globules which is seen to continue for several seconds in a drop of blood placed on a glass under the microscope. The fallacy of this opinion is, however, completely

* C. H. Schultz, der Lebensprocess im Blute. Berlin, 1822.

† Meyen, Isis, 1828, 394, and the review by an anonymous writer,—Isis, 1824, 3, —are especially worthy of being consulted on this subject.

‡ Mayer, Supplemente zur Lehre vom Kreislauf. Bonn, 1827.

§ [The hypothesis here alluded to is partly discussed by the author in this place; but the translator, to avoid repetition, has placed all the arguments together in the chapter on the circulation in the capillaries.]

proved by the fact, that these momentary whirling motions can be seen, as I have often witnessed, in drops of blood which has been long removed from the body. Thus, for example, in a drop of frog's blood which has been taken from the animal twelve or twenty-four hours, and from which the fibrin has been removed, we can distinguish by means of the microscope the same motions of the red particles as in fresh blood; they cannot therefore be dependent on vitality. In the blood of warm-blooded animals such motions may also arise from evaporation. It is probable, likewise, that the slight change of form which every drop of fluid spread on a glass plate suffers at the edges, and sometimes quickly, has considerable influence on these motions. I have also often remarked in a drop of diluted frog's blood, whether when fresh, or after it had been kept several hours, the fibrin having been removed, that, after the cessation of the first described motion, single contiguous globules approach each other very slowly. This, however, is probably also dependent on physical causes, such as evaporation, and the attraction of adhesion.

Motions in coagulating blood.—Heidmann* has described contractions and dilatations which he has observed in the blood during coagulation. I have myself, however, been able to detect no dilatation, and no other contraction than the gradual imperceptible contraction of the coagulated fibrin. The contractions which Tourdes and Circaud described to be produced in the fibrin by galvanism have been proved, even by Heidmann himself, not to exist, and I certainly saw nothing of the kind in galvanising the liquor sanguinis of the frog's blood.†

Is the blood endowed with life?—The question whether the blood be a living fluid or not, calls to mind a critical state of our science. Everything which evidences an action which cannot be explained by the laws of inorganic matter, is said to have an organic, or, what is the same thing, a vital property. To regard merely the solids of the body as living is incorrect, for there are strictly no organic solids; in nearly all, water constitutes four-fifths of their weight. Although then organic matter generally be considered as merely "susceptible of life," and the organised parts as "living," yet the blood also must be regarded as endowed with life, for its actions cannot certainly be comprehended from chemical and physical laws. The semen is not merely a stimulus for the fructification of the egg, for it impregnates the eggs of the batrachia and fishes out of the body; and the form, endowments, and even tendencies to disease of the father are transferred to the new individual: the semen, therefore, although a fluid, is evidently endowed with life, and is capable of imparting life to other matter. The impregnable part of the egg, the germinal membrane, is a completely unorganised aggregation of animal matter, and nevertheless is animated

* Reil's Archiv. vi. 425. † See experiments related at note, p. 137.

with the whole organising power of the future being, and is capable of imparting life to new matter, although soft and nearly allied to a fluid. The blood also evidences organic properties; it is attracted by living organs which are acted on by vital stimuli; there subsists between the blood and the organised parts a reciprocal vital action, in which the blood has as large a share as the organs in which it circulates. The fibrin of the blood effused in inflammation is at first fluid, and forms, as it becomes solid, pseudo-membranes; but this exudation, by means of a mutual vital action exerted between it and the organs by which it is poured out, becomes organised and traversed by blood and vessels. The blood itself has, therefore, the properties of life, and this is the case with all the animal fluids except those which are the means of carrying out of the body the effete material, such as the urine and carbonic acid. The saliva and the bile exert an assimilating action on the food, the different organs perform the same functions with regard to the blood, and here there is no clearly defined limits between substances capable of life and those endowed with it. Those substances, however, in which life is least evident, remain susceptible of life as long as they are not chemically changed.

c. *Formation of the blood.*

The materials for the formation of the blood are the contents of the absorbent system, namely, the transparent lymph and milky chyle, which convey into the thoracic duct, and thus into the blood,—the former fluid, those nutritive matters taken up from the intimate structure of the organic body; the latter, those absorbed from the intestinal canal. The lymph and chyle contain albumen and fibrin in solution, but these substances are in less proportion in them than in the blood. The lymph has the greatest possible resemblance to the liquor sanguinis of the blood, which also contains lymph and albumen in solution; so that the liquor sanguinis may be correctly termed the lymph of the blood, while the blood may be regarded as lymph with red particles, or the lymph as blood without red particles. The chyme or digested food in the intestines contains albumen in solution, but no coagulable fibrin; the latter substance is formed in the absorbents, and thence is poured into the blood. It is a remarkable fact, which I have observed to be nearly constant, that in frogs kept long without food, the blood frequently loses its property of coagulation, and that in these cases the lymph, which usually coagulates quickly like the blood, also does not coagulate. In winter, however, the blood of the frog often coagulates, although not completely; but in all cases where their blood does not coagulate perfectly, the coagulation of the lymph is also not so firm. I find this to be the case in many frogs dug out from the ground in winter, although they are quite active. Lymph and chyle contain somewhat less solid matter

than the blood, and especially less fibrin; 100 parts of chyle, according to Tiedemann and Gmelin, contain from 0·17 to 1·75 parts of dry fibrin. Chyle is less distinctly alkaline than the blood. There is a certain quantity of uncombined fat in the chyle, which appears to become more intimately combined in the blood. Iron also is in a state of less intimate combination than in the blood, and can be detected, according to Emmert, by adding tincture of galls to chyle previously treated with nitric acid. [The globules of the lymph will be particularly described at a future page;* we have already seen that they differ both from the red particles of the blood, and from the nuclei of the red particles, in form as well as in size, but they resemble exactly the more scanty globular bodies which are contained in the blood mixed with the red particles.]

Autenrieth supposes that the chyle poured into the circulation, is converted into blood in the course of ten or twelve hours, because within this period the serum is frequently observed to be milky. It is probable, however, that the change is effected still more slowly; for, as I have already remarked, when the coagulation of the blood is retarded by the addition of sub-carbonate of potash, the supernatant fluid from which the red particles have subsided, is often somewhat turbid and milky.

In what part of the system the red colouring matter or envelope of the red particles of the blood is produced, is quite unknown; it is not present in the chyle and lymph; a slight trace of it only being sometimes detectable in the thoracic duct. Respiration seems to have a share in its production. Hewson's hypothesis that the red colouring matter is formed in the spleen and in the lymph of the spleen, which is sometimes of a dirty red colour, is without foundation; the spleen may be extirpated from living animals without bad consequences.

It is quite impossible to imagine the cause of the different forms of the red particles in the different classes of vertebrate animals. There are no similar elementary forms in the whole body.

Formation of the blood in the ovum.—In the incubated egg the sole material for the first formation of the blood, is the substance of the germ or germinal membrane, which itself grows by assimilation of the fluid of the egg, or the yolk. It may be distinctly observed, that the blood is first generated in the germinal membrane before the vessels and before the glands are formed, which in the adult have some influence on the formation of the blood. The germinal membrane, at first simple, is after a short time found to consist of an upper thinner or serous layer, and an under thicker or mucous layer. Around the first trace

* [The description of the lymph globules, and the comparison of them with the red particles of the blood were repeated here, but have been omitted by the translator.]

of the embryo, which is visible in the centre of the germinal membrane, a transparent space or area pellucida is formed, while the part of the germinal membrane nearer the circumference remains opaque, and this opaque portion again is soon divided by a line of separation into an outer and inner space; these changes take place in the ovum of birds, in from sixteen to twenty hours.* That division of the opaque portion of the germinal membrane, which is immediately within the line of separation above mentioned, and which surrounds the innermost portion or transparent area, is called the area vasculosa, because within it the blood and vessels are formed. As far as the area vasculosa extends, there is found between the two layers of the germinal membrane a granular deposit which soon becomes arranged in granular close islets separated by transparent interspaces, in which first a yellowish, afterwards a red fluid,—the blood,—collects. The presence of blood is first distinctly observable in the periphery of the area vasculosa.

The red particles of the blood in the embryo of the bird for the first few days after its appearance in the germinal membrane, are, according to Prevost and Dumas, round, and do not begin to assume the elliptic form before the sixth day; on the ninth day they are all elliptic.† Hewson, Schmidt,‡ and Doellinger have made a similar observation. The same fact has been observed also by Baumgärtner§ in reptiles and fishes, and by E. H. Weber|| in the tadpole.

Baumgärtner describes the formation of the red particles of the blood in the following manner:—The corpuscules, he says, are at first not elliptic or flattened, but globules composed of a number of smaller globules similar to those of the yolk of the egg; they gradually become transparent, and at the same time this granular state disappears; the transparent ring is then developed, and the nucleus formed. The elliptic form is gradually assumed. Weber also describes the corpuscules of the blood in very young tadpoles to be composed of several smaller granules. Baumgärtner supposes that the smaller granules here mentioned are derived from the yolk. Another mode in which Doellinger¶ and Baumgärtner imagine the red particles of the blood to be formed, both in young and adult animals, is the separation of particles from the parenchyma.

It is evident that in the embryo the blood is formed from the substance of the germinal membrane, which assimilates to itself the fluids of the egg, and that no particular organ is then required; for at that period no organs, such as intestinal canal, liver, spleen, or lungs, exist. This fact teaches us that we must not expect to discover the

* V. Baer; de ovi mammalium genesi.

† Froriep's Notiz. 175.

‡ Über die Blutkörner. Würzburg, 1822.

§ Über die Nerven und das Blut. Freiburg, 1830.

|| Loc. cit. iv. 478.

¶ Denkschr. der Akad. zu München, vii. 169.

process of the formation of the blood and its red particles (from the globules of the chyle?) in any special organs of the adult animal; indeed it is very probable that the chyle is converted into blood, in the adult also under the influence of the same general vital conditions which are in action in the incubated egg.

Action of respiration in the production of blood.—Respiration seems to have an essential share in the process, inasmuch as even in the incubated egg the influence of atmospheric air, and in aquatic animals that of water containing air, seems to be quite necessary for the developement of the embryo, and the air suffers the changes which ordinarily take place in respiration. From an important observation of Von Baer * it would seem probable that in the original formation of the blood in the germinal membrane in mammalia, the respiratory change is by no means essential; for Baer has seen the ovum of the bitch, at a period when the area vasculosa of the germinal membrane already contained blood and vessels, quite free in the cavity of the uterus, and without any connection with it, by which the function of respiration could be supplied: Burdach supposes that under these circumstances the plug of mucus closing the uteri of pregnant mammalia allows the passage of air to the ovum. The state, in which there is no vascular connection with the uterus, is indeed a permanent condition of the ovum of the marsupial animals.† In the fœtus of mammalia there is, however, even at a later period, no distinct difference between arterial and venous blood,‡ and the want of respiration is supplied by a process of another kind, which is maintained by means of the union of the ovum with the uterus, but of which the nature is unknown.

Perhaps respiration is not immediately necessary to the formation of the colouring matter. The necessity of respiration is indeed supported by the fact, that the coagulum of chyle is in some rare cases (though I have not myself witnessed it) reddened by exposure to the atmosphere. The observation that the chyle in the horse (rarely in any other animal when obtained pure) has a red tinge in the thoracic duct, cannot at present be adduced as a proof that the formation of the colouring matter commences in the lymphatic vessels, for it is very possible that a few red particles may regurgitate into the ductus thoracicus from the venous trunk and mix with the chyle. I cannot confirm the observation of Goeze, which Treviranus adduces, namely, that the blood in the hybernating frog in its torpid state in winter is whitish; although throughout the winter season, when the weather allows of digging, I obtain frogs which have been dug from the earth, although certainly not torpid.

That the blood during respiration undergoes a change necessary to

* Loc. citat.

† Owen. Philos. Transact. 1834, p. 2.

‡ See the chapter on the respiration of the ova of animals.

the preservation of life, is proved by death occurring whenever this function is interrupted. The nature of the change, however,—the influence which respiration has on the formation of the blood,—cannot be accurately determined; we have no means of ascertaining whether the blood would acquire its red colour and the other properties connected with this colour,—whether any red particles would be developed, if respiration was not performed. A very small portion only of the changes which take place in the passage of the blood through the lungs is recognisable, and that is the change of the dark red colour of the blood to a bright red, which during its passage through the capillary vessels of the body generally is reconverted to a dark red. But unfortunately even here it is the change of colour only that we are acquainted with, and not the material change which accompanies it.*

It is still uncertain in what part of the body the carbonic acid which is expired during respiration, is formed. The changes produced in the air by respiration, as far as regards the bulk of the component gases, can be as well explained on the supposition that the carbonic acid is formed in the lungs by the direct union of the carbon of the blood with the oxygen of the air, as on the theory that the carbonic acid is formed in the course of the systemic circulation, and especially in the capillaries. But it is at least probable that a part of the oxygen of the air is absorbed by the blood; and as no oxygen can be again separated artificially from arterial blood, it appears to enter into a state of chemical combination with it. The proportion of nitrogen in the air respired is not essentially altered.

The absorption of oxygen and the separation of a portion of carbon, therefore, are the causes to which arterial blood owes its property of being the sole stimulus of living structures. Venous blood which has not undergone this change has a poisonous action on the organs of the body, particularly on the nervous system, and annihilates their irritability; its action being similar to that of carbonic acid, sulphuretted hydrogen, carburetted hydrogen, and some other gases, by which the irritability of the organs of the body is destroyed, and by most of which the arterial blood is darkened in colour. Cuvier* supposes, indeed, that the arterial quality of the blood is diminished even during its course from the heart to the capillary vessels, by reason of some change of composition which it undergoes, and thus explains the inferior degree of vitality possessed by parts distant from the heart.

Another difficulty which we are quite unable to solve is, whether the venous blood is incapable of supporting life from having lost something which arterial blood possesses, or from having suffered some

* See the comparison of arterial and venous blood in the chapter on the changes which the blood undergoes in respiration.

† Verg. Anat. p. 147. Anatomie comparée.

noxious change in the combination of its elements, the natural combination being in the latter case again restored by respiration and the separation of the carbonic acid. It is very remarkable, however, that the venous blood of the embryo of mammalia, although strictly speaking it does not respire, has not this injurious, as it were a suffocating, influence on life, whether it be that this injurious quality cannot be developed until respiration, and consequently the reciprocal action of true arterial blood with the tissues take place, or that the want of respiration is supplied by the connection of the embryo with the mother.

Since the blood is constantly throwing off carbon in the process of respiration, it might be thought that the relative proportion of nitrogen in the body ought to increase. Cuvier believed that animal matters are in this way more highly animalised, because the characteristic element of animal substances is the nitrogen they contain. If this were correct, the flesh of a living animal must contain more nitrogen than the flesh of animals from which it is nourished, which involves a contradiction. Respiration viewed in this way would be no advantage to carnivora, and would be more necessary to herbivora, because their food contains less nitrogen. But the relative increase in the quantity of nitrogen in the animal body which the separation of carbon in respiration would produce is generally not permanent, for an excess of nitrogen is being constantly excreted from the body in the urea and uric acid of the urine, which contain more nitrogen than any animal substance.

The influence of the spleen, suprarenal capsules, and of the thyroid and thymus glands on the formation of the blood, is not at all understood.*

Influence of the excretions on the formation of the blood.—The separation from the blood of certain matters which are afterwards excreted from the animal economy, has a great share in preserving the normal composition of the circulating fluid. Some of the matters here alluded to have been introduced from without, and are either in themselves useless, or are in too abundant quantity. Of these, water is got rid of by exhalation from the lungs and skin, and by the urine; the mineral substances are expelled chiefly by the urine; and matters containing an excess of carbon, nitrogen, oxygen, or hydrogen, are eliminated in various ways:—the carbon by the lungs; combinations containing much carbon and hydrogen by the liver; and those in which the nitrogen is abundant by the kidneys. Other of the substances that disturb the normal constitution of the blood are newly formed in the body, and, being taken up into the blood, must be subsequently excreted from it. Such seem to be several of the matters contained in the urine. This shows how the proper composition of the blood when once established is maintained.

Another question is, whether the separation of certain ingredients from the new nutritive matter which the blood derives from the food,

* See Book II. section 2.

contributes essentially to the original production of the normal composition of the blood? The lithic acid of the urine,—a product containing a large quantity of nitrogen,—is derived without doubt, at least in part, from this source; for its quantity in the urine is increased by merely taking animal food, or substances containing a large proportion of nitrogen; and in the urine of herbivorous mammalia it does not exist, but is replaced by hippuric acid (urino-benzoic acid). It is not yet known whether lithic acid exists in the blood, and is merely separated from it by the kidneys, or whether it is first formed in the urinary organs; although under certain circumstances it is deposited from the blood in different parts, for instance, in the neighbourhood of joints, forming gouty concretions.

Urea is not formed originally by the organs which excrete it,—namely, the kidneys; for Prevost and Dumas have shown that it can be detected in the blood when the kidneys have been extirpated, so that the reason why this substance is not found in healthy blood, is that it is separated from it by the kidneys as fast as it is formed. On the third day after the extirpation of both kidneys, the following symptoms arise; brown, copious, very fluid evacuations from the intestines, and vomiting, fever, with the temperature raised to 110° Fahr., sometimes, however, depressed to 92° Fahr.; the pulse becomes small, and quick, and rises to 200 beats in a minute, the breathing frequent and short, and at last laboured. Death ensues between the fifth and the ninth day. In Mayer's* experiments it took place in from ten to thirty hours, being preceded by tremblings and convulsions. Effusion of clear serum is found in the cavities of the brain, the bronchi are full of mucus, the liver inflamed, the intestinal canal full of fluid fæces coloured with bile, the urinary bladder much contracted. The blood of the animals experimented upon—dogs, cats, and rabbits—was more watery than natural, and contained urea, which was extracted by means of alcohol. Five ounces of the blood of a dog, which lived two days after removal of the kidneys, afforded more than twenty grains of urea; two ounces of cat's blood yielded ten grains.† Vauquelin and Segalas‡ have confirmed this discovery. In their experiments the blood was evaporated to dryness, the residue washed, and the water evaporated; the mass left was then treated with alcohol, and this again evaporated. The water, however, must be evaporated at a low temperature, under the vacuum of the air-pump, with sulphuric acid. They thus obtained from the blood of a dog, whose veins were opened sixty hours after the operation, $\frac{1}{400}$th part of urea. Urea and uric acid contain more nitrogen than any other known organic substance.||

* Tiedemann in Treviranus, Zeitschrift für Physiol. 2, 2, 278.
† Biblioth. Univers. xviii. 208. Meckel's Archiv. viii. 325.
‡ Magendie's Journal de Physiol. ii. 354. Meckel's Archiv. viii. 229.
|| See the Section on Secretion, chapter 8.

The presence of urea in the blood may be accounted for in two ways. First, it may be supposed to be formed as a useless compound of the superfluous elements in the conversion of the food into the essential components of the blood; or, secondly, it may be conceived that it is an effete product of the change of material that is constantly taking place in the organised parts of the body. The first conclusion might be suggested by the circumstance that Tiedemann and Gmelin, in one of their experiments on chyle, observed that the muriate of soda mixed with the osmazome of the chyle crystallised into octahedrons instead of cubes, while in other cases it took the cubic form; for urea is known to have the power of altering the crystallisation of this salt to the octahedric form.* But there are other facts which render this conclusion improbable. Urea is formed in a certain quantity by reptiles, which have fasted even for months; and in the urine of a madman who had fasted eighteen days, Lassaigne found all the components of healthy urine.† Moreover, in the urine of herbivorous animals, (whose food contains very little nitrogen,) there is a considerable proportion of substances containing nitrogen, such as urea. There is certainly no doubt but that the kidneys separate from the blood the useless matter derived from the food; for the urine varies in composition, according as the food varies; for instance, it contains more uric acid when the food consists of animal matter. In birds which feed on substances containing no nitrogen, the excrements contain much less white matter, or uric acid, than when they are fed upon white of egg.‡ In the composition of the urine of herbivorous and carnivorous animals, there is a difference corresponding with the difference of their food; the urine in the former animals contains hippuric acid, instead of uric acid, and is alkaline instead of acid: the urine of birds generally contains superlithate of ammonia; but the urine of birds feeding on vegetables contains no urea. There is, however, also no doubt but that certain components of the urine are also formed from effete elements of the blood, or of the solids of the body. Since then it appears certain that the products of the urine are not merely separated from the blood to give the latter its proper elementary composition, we may suppose that the urea is produced by component parts, either of the blood or of the tissues of the body becoming unfit for further use, or that during the reciprocal action of the arterial blood and the organs on each other—an action so necessary to life—certain components, either of the blood or of the tissues of the organs, are converted into useless combinations, being in fact chemically changed. It is, however, improbable that the latter is the mode of their formation, from the circumstance that lithic acid at least

* Tiedemann und Gmelin, Versuche über die Verdauung, ii. 91.

† Journ. de Chim. Méd, 272.

‡ Tiedemann und Gmelin, die Verdauung, ii. 233.

is formed in the embryo. It is found in the allantois not only of birds, but also of mammalia; and the fœtus of mammalia, while in the uterus of the mother, does not respire in the proper sense of the word, and therefore has no arterial blood, although the want of respiration is supplied by the connection of the fœtus with the mother. Besides, the formation of the substances of which we are here speaking commences extremely early in the embryo. The kidneys, it is true, are not formed in the incubated egg of the bird till about the sixth day; and in the embryo of fishes and salamanders, according to my researches, not till the state of larva has succeeded that of the embryo; but at a remarkably early period there are other organs in their place, namely, the Wolffian bodies, first accurately described by Rathke and myself. These organs consist of cæca communicating with an excretory duct; in the embryo of birds they exist as early as the third day; and, according to my observations, form from the blood a true secretion of a yellow colour, similar to the urine of birds; while the allantois, as Jacobson* discovered, contains at the same time, namely, a very few days after the commencement of incubation, lithic acid. The Wolffian bodies are found in the embryo of all vertebrata with the exception of fishes: they disappear in some animals earlier than in others; in the batrachian reptiles not until they have acquired the state of larva; in birds at the time of hatching, or even later; in the mammalia very early, and earliest of all in man.†

By means of the skin the blood throws off lactic acid, lactate of ammonia, muriate of ammonia, and carbonic acid. Lactic acid, which also passes off by the urine, is, according to Berzelius, an universal product of the spontaneous decomposition of animal matters within the living body; it is formed in great quantity in the muscles, is neutralised by the blood and its alkali, and separated in the kidneys with acid urine.

The important office which the bile performs in the assimilation of animal matters in the intestines is not better understood. The fact of its being poured, both in vertebrata and in mollusca, into that part of the canal where the formation of the chyme is completed, proves that it is not excrementitial merely; besides its most abundant component, picromel, has evidently some connection with the assimilation of the chyme, for it is not found in the fæces. Some, however, of the components of the bile are certainly excrementitious matters thrown off from the blood; and these are essential components of the fæcal matter. Such are the resin of the bile, cholesterine, and the colouring matter of the bile, of which no traces are found in the chyle. The liver, therefore, frees the blood from an excess of matters containing carbon and hydrogen, and from fatty matter, while the kidneys remove from it the superabundance of

* Meckel's Archiv. viii. 322.

† J. Mueller, Bildungsgeschichte de Genitalien. Dusseldorf, 1830.

those materials which contain a large proportion of nitrogen. The colouring matter of the bile, which is also excrementitious, contains nitrogen. The lungs and liver are so far analogous, inasmuch as both separate from the blood substances containing a large proportion of carbon. In the former case, however, it is already combined with oxygen; in the latter case it is still in the oxidisable state. Earlier physiologists, and more recently Antenrieth, and particularly Tiedemann and Gmelin, have directed attention to a certain vicarious action in the functions of the lungs and liver. Although it does not appear that the size of the liver is throughout the animal kingdom in the inverse ratio of the size of the respiratory organs, yet pathological observations are certainly in favour of the existence of such a relation.

The excretory action of the liver is exerted also under circumstances in which digestion is not carried on. For although the liquor amnios is swallowed by the fœtus, it is only during the latter period of gestation; while the liver is developed and secretes at a very early stage of fœtal life, and the bile, although less bitter and less coloured at that period, contains, according to Lassaigne,* a green resinous matter and a yellow colouring matter, but no picromel. In fact, it is the excrementitious matter of the bile of the fœtus, which collects together with intestinal mucus in the lower part of the canal, forming the meconium. It appears from the experiments of Tiedemann and Gmelin that the secretion of bile is carried on in the same way in hybernating animals during their state of torpor. These inquirers also state, that Cuvier has observed in many molluscous animals that a small portion only of the bile is poured into the upper part of the intestinal canal; while the rest is evacuated by a separate duct either into the cæcum, as in the aplysia, or near the anus, as in the doris and tethys. It is, however, at present very doubtful whether the secretion which in the last two animals is poured out near the anus, is bile, and it certainly cannot be the greatest part it. I have examined several large examples of the doris, and found the excretory duct which Cuvier has discovered. It appears, however, to arise, not, like the bile ducts, from the clustered vesicles of the liver; but by numerous branches, some of which run between the lobes of the liver, from a reticular tissue which is extended over its whole surface, while one large trunk comes from the interior. To me it appeared that two kinds of fluids are here separated from the blood, which is distributed through the mass of the liver, there being perhaps a special apparatus for the formation of each secretion. In its point of termination, this duct discovered by Cuvier is analogous to the excretory duct of the saccus calcareus of snails, but its origin is certainly very different.

The frequency of diseases of the liver and the intestinal canal in tropical climates and hot seasons, and of affections of the liver and abdomi-

* Ann. de Chim. et de Phys. xvii. 304.

nal organs in damp marshy air, is still unexplained. Could it be ascertained that these circumstances in some way impede the circulation and cause congestions, it would be easy to conceive why the liver and intestinal canal should suffer most in those cases; for the circulation in these viscera must be doubly impeded, the blood of the intestinal veins and porta having to circulate through a second capillary system, namely, that of the liver, before it reaches the general circulation. Tiedemann and Gmelin maintain that the increased secretion of bile in tropical climates is required to compensate for the diminished purification of the blood in the lungs; many persons supposing that the function of the latter organs is rendered inefficient on account of the rarification of the air by the heat. Stevens* thinks this assumption incorrect; for in the West Indies, he says, the inhabitants of the smallest islands, which are the driest and hottest, but in which there are no stagnant waters, are free from diseases of the liver and increased secretion of bile, and these diseases are prevalent in hot climates only where there is a marshy atmosphere (malaria).

SECTION II.†

Of the Circulation of the Blood and of the Vascular System.

CHAPTER I.

OF THE FORMS OF THE VASCULAR SYSTEM IN THE ANIMAL KINGDOM.

Peculiar chemical changes of an organic nature are effected in the blood in special organs of the body. All parts of the system, however, require a supply of blood which has undergone these changes, and hence the circulation of this fluid is indispensable.

The circulation of the blood was discovered in the higher animals by Harvey in 1619. It has since been found to have a much more extended existence; and although it cannot be asserted to be a universal character of all animals, yet at every advance of observation new traces of vessels are discovered in the most simple beings. Ehrenberg has described them in the rototoria, and even microscopic minuteness does not appear to preclude the existence of this complex structure. The following are the more important facts relative to the different forms of the vascular system in the animal series.

Circular currents in the lower animals.—In several of the lowest tribes of animals there are circular currents similar to those in the chara. Thus

* Observations on the Healthy and Diseased Properties of the Blood, London, 1832, p. 59.

† [The translator has made considerable alteration in the arrangement of the contents of this chapter.]

Nordmann has observed in the envelope of the alcyonella diaphana small isolated circulations, and similar currents have been described by Carus between the ambulacra of the sea urchin; the ascending and descending motions in the stem of the sertularia observed by Meyen* and Lister are of the same kind. Lister asserts that they are connected with the stomach, and change their direction from time to time. Ehrenberg† also has observed circular currents of granules in the medusa and in the retractile fibres on the dorsal aspect of the asterias. These phenomena seem to be wholly independent of the action of a heart, but they have not hitherto been sufficiently investigated, to lead to any important conclusions with reference to the circulation in the higher animals. It is possible that they depend on the motion of cilia within the vessels.

Circulation in acalepha and entozoa.—In the medusa tribe the fluids are distributed through the body by means of vessel-like ramifications of the digestive sacs. In the planaria and the trematoda the intestine is ramified like a vessel. But, in addition to this, these animals possess an independent vascular system, which however in the distoma and diplostoma appears to have an external opening at the posterior part of the animal.‡ In the diplozoa, which also belong to the order trematoda,—intestinal worms provided with suckers,—Nordmann has described two vessels on each side in which the blood moves in opposite directions. It appears from the statements of Ehrenberg and Von Nordmann that in these animals,—the trematoda,—the motion of the fluid is not dependent on contractions of the vessels themselves; it may possibly be effected simply by the contractions of the entire body, if the vessels are furnished with valves arranged all in a certain direction.

In the lowest animals of which the circulation has been accurately observed, as in the planaria, echinodermata, and leech tribe, the motion of the blood is effected by one, two, or more contractile vessels. These vascular trunks are however neither arteries nor veins, but are in part contractile hearts, which force the blood into anastomosing branches.

Holothuria.—The vascular system discovered by Tiedemann in the holothuria seems to be of this nature; it is situated in common on the intestine and on the respiratory organ, and is independent of the system of water tubes with which the skin of this animal is provided for the erection of the tentacula.||

In the annelides there is a progressive contraction of the vascular trunks, advancing regularly in one direction, and thus, according to Dugès, driving the blood in a continued circle in the larger vessels; while at the same time the circulating fluid is thrown alternately from side to side through the transverse anastomosing branches, one trunk

* Nov. Act. Nat. Cur. vol. xvi. Suppl.

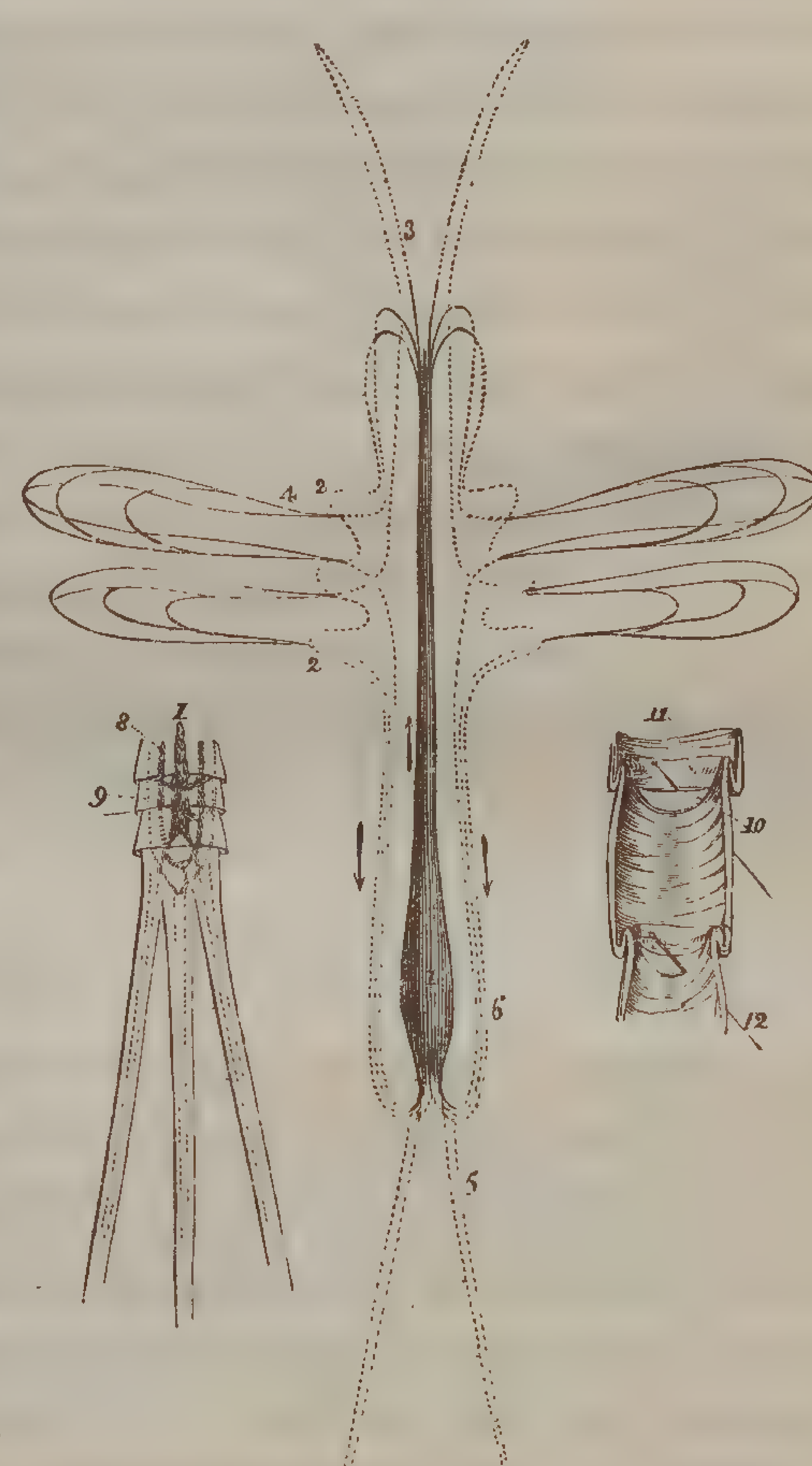
† Müller's Archiv. 1834, 571.

‡ Nordmann, Micrograph. Beiträge, 1832, i. pp. 39. 98.

|| Tiedemann, Anatomie der Röhrenholothurie, &c.

being filled while the other contracts, as is seen in the hirudo vulgaris.* When the principal trunks lie at the sides, as in the hirudo family, the direction of the circulation is horizontal; when they are situated above and below, as in the lumbrici, arenicolæ, and naïdes, it is vertical. From my own observation, I thought that in the hirudo vulgaris both the lateral vessels alternately emptied themselves from behind forwards. Dugés, however, maintains that the motion is progressive in a continuous circle. The respiratory organs of the annelides, whether they be branchial tufts as in the arenicolæ or sandworms, or pulmonary vesicles, receive their blood, like the other organs of the body, from branches of the main vessels. In the nereides, Professor R. Wagner has described two longitudinal trunks; one on the dorsal aspect, which pulsates and impels the blood from behind forwards; the other on the abdominal aspect lying upon the nervous cord under the intestines; the latter does not pulsate or contract: in addition to these there are transverse vessels, superior and inferior, corresponding to the rings of the body; of these the inferior, which arise from the abdominal vessel and pass to the feet or branchiæ, pulsate beautifully; the superior branches, which commence in the branchiæ and terminate in the dorsal vessel, do not pulsate.

Fig. 1.‡



Insects.—In animals in which there is but one contractile vessel, the circulation is simple but perfect; the fluctuating motion of the blood from side to side does not exist, and there are distinct arterial and venous currents. Such is the circulation which Carus † has discovered in insects (fig. 1.): the blood flows in a simple circle, being impelled forwards by the dorsal vessel; it returns in the opposite direction through the body, and again enters the dorsal vessel.

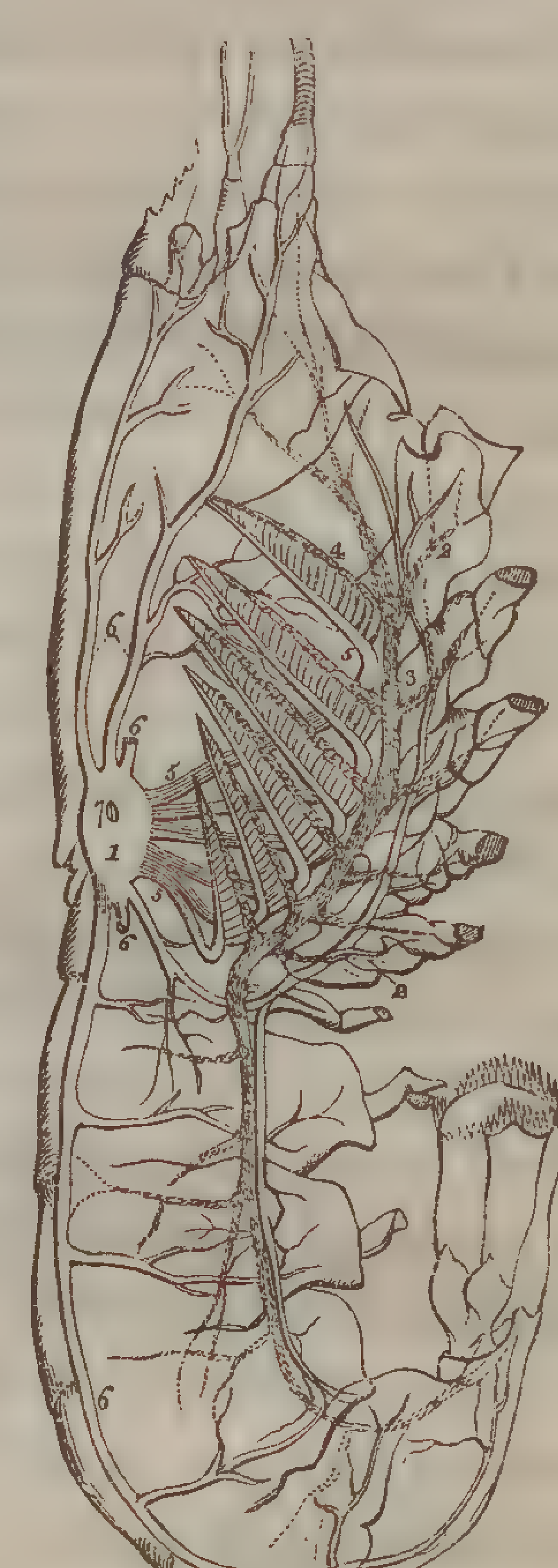
* J. Mueller, Meckel's Archiv. 1828; and my observations on the Arenicola in the 4th vol. of Burdach's Physiol. On the subject of the annelides generally, consult Dugès, Ann. des sc. nat. t. xv.

† Entdeckung eines Blutkreislauf, &c. Leipzic, 1827. Nov. act. nat. cur. t. xv. p. 2.

‡ [Circulation in the insect after Carus, Wagner, and Strauss.—1. Dorsal vessel; 2. simple loops to the feet; 3. simple arterial and venous currents of the antennæ; 4. anastomosing vessels in the wings; 5. simple currents in the caudal appendages, arising from and returning into the lateral venous currents (6), which brings back the blood to the dorsal vessel; 8. and 9 are the two lateral venous currents described by Wagner;

The currents are very simple and do not ramify; the feet, for example, have each two currents running in opposite directions, the arterial being reflected uninterruptedly into the venous, forming a loop. It is at present unknown whether the internal organs of insects receive any vascular currents. As early as 1824, however, I discovered and described a connection between the oviducts and the dorsal vessel of many insects.* Wagner also has since observed these connections, but agrees with Carus, Treviranus, and Burmeister, in considering them not to be blood-vessels. Whatever they may be, their existence is indubitable; in two insects however I have not succeeded in finding them. Wagner has added new facts to Carus's discovery of a visible circulation in insects; he has seen the particles of the blood flowing in two venous currents (fig. i. 8, 9) at the sides of the intestine and dorsal vessel, probably in canals without membranous parietes, and at the same time he has seen particles of the blood from these currents enter the dorsal vessel through lateral clefts. Strauss had previously described these lateral clefts at the divisions of the dorsal vessel: he says, that in the cockchaffer—melolontha vulgaris,—this vessel consists of eight chambers which communicate by two-lipped valves (fig. i. 10, 11) directed forwards, so as to allow the blood to pass from behind forwards.†

Fig. 2.‡



Arachnida and crustacea. — The circulation in the arachnida and the lower crustacea, such as the aselli and daphniæ, according to Zenker and Gruithuisen, is nearly as simple as in insects. There is no distinct pulmonary circulation; but as in the arachnida with pulmonary sacs, a part of the blood is aerated in the respiratory organs in its course through the general circulation. In the arachnida, with tracheal organs of respiration as well as in insects, the blood is aerated by the tracheæ which ramify most minutely in all parts of the body. In the higher crustacea there is either a long tubular heart as in the squillæ and allied genera, or a short wide one as in the decapoda. (Fig. 2.)

10. is the posterior, and 11. the anterior of the valves discovered by Strauss; a bristle is passed through the cleft between them; 12. a bristle passed through another of the lateral clefts, from which the lower valve has been removed.]

* Nov. act. nat. t. xii. 2. Compare Wagner's observations in the Isis, 1832, 320.

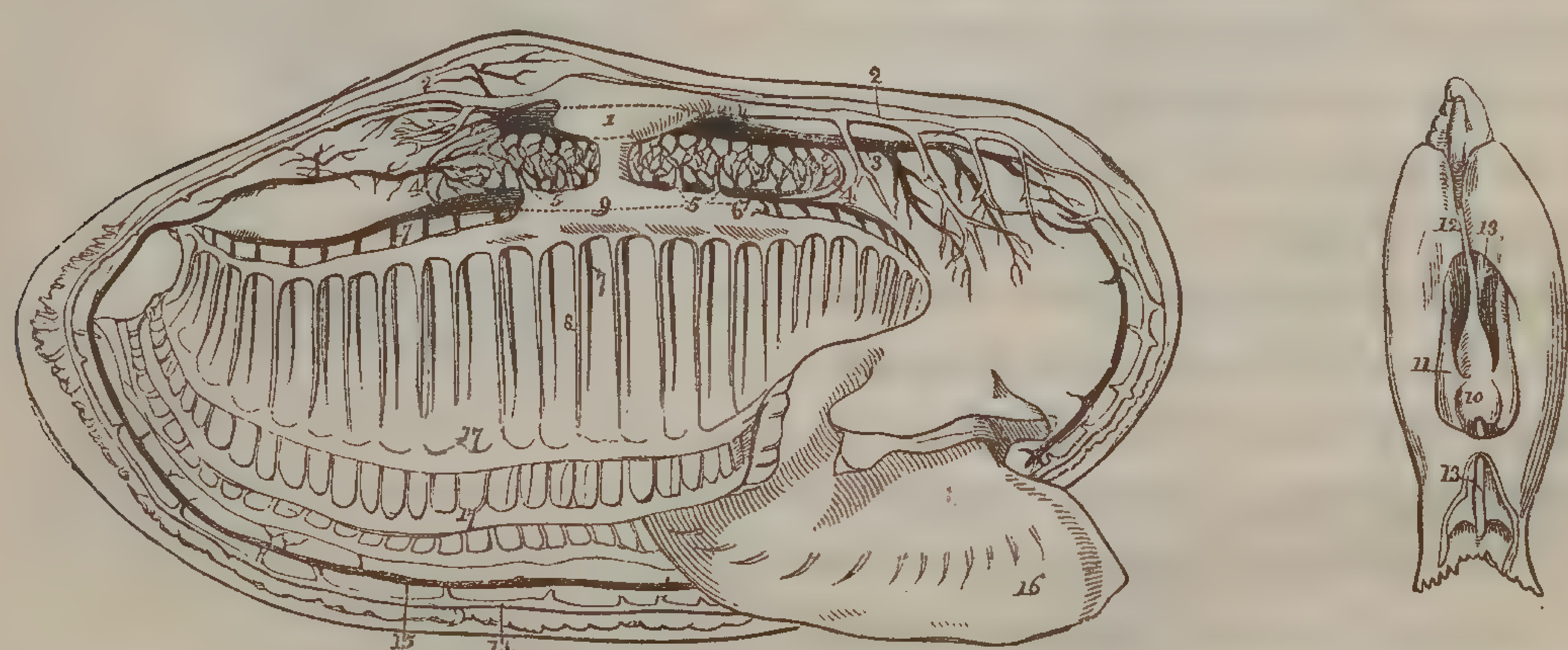
† Strauss, Considérations générales sur l'anatomie des animaux articulés, &c. Paris, 1829.

‡ [Circulation in the lobster copied from the diagram given by Dr. Allen Thomson in his excellent paper on the circulation, in the Cyclopædia of Anatomy.—1. Heart; 2.

The blood is collected from the body by veins, from which it is carried into the branchiæ, returning from these to the heart, which again distributes it to the body. This course of the blood was discovered by M.M. Edwards and Audouin, and while at Paris I satisfied myself of its existence by injecting a lobster. I agree with Meckel that Strauss is incorrect in considering the membranous covering of the heart of these animals to be an auricle.*

Mollusca.—The circulation in the mollusca is similar to that in the crustacea. In the naked *acephala* or *tunicata*,—as the ascidia and salpa,—the veins from the branchiæ enter the ventricle immediately. In the *conchifera*, as well as in most *gasteropoda*, the blood is first collected in an auricle, (in the conchifera there are two auricles,) and thence passes to the ventricle.

Fig. 3.‡



In the majority of the mollusca all the venous blood circulates through the branchiæ before reaching the heart, but in the conchifera (fig. 3) Bojanus† says, that, after passing through the hollow organ provided with an excretory duct,—which he considers to be a lung, later anatomists to be a kidney,—it is chiefly distributed to the branchiæ, while a portion

systemic veins which convey the venous blood to the sinus (3.) at the base of the branchiæ; 4. branchial arteries arising from the sinus; 5. branchial veins by which the aerated blood is carried to the heart: 6. the systemic arteries; 7. depression on the surface of the heart. There are two such depressions, one on each side. Lund and Strauss suppose that they are openings through which blood enters the heart from the cavity of the pericardium or auricle. Mr. Owen also believes that they are openings closed by valves.]

* See Ann. d. sc. nat. 1827, tab. 24—32.

† Isis, 1819.

‡ [Diagram of circulation in the fresh-water muscle, adapted from the drawings of Bojanus.—1. Ventricle; 2. systemic arteries; 3. systemic veins,—14. is the large artery, and 15. the vein, which run near the margin of the mantle. The veins carry the blood in part directly to the organ (4), which is called the kidney, and in part to a venous sinus on the superior surface of the organ, to which it is afterwards distributed; 5. veins by which a portion of the blood is returned from the kidney immediately to the auricle, while the rest is poured into the sinus (6), from which the branchial arteries (7) arise; 8. branchial veins; 9. auricle. In the smaller figure are seen the position of the two auricles (11) with relation to the ventricle (10), and the course of the intestine (13) through the ventricle; 12. is the principal arterial stem to the anterior part of the body.]

reaches the auricle without entering the respiratory organs. Treviranus* again says, that a portion of the blood returning from the branchiæ in the bivalves circulates through the spongy organ before it gains the heart, just as in gasteropoda (limax and helix) the blood from the lungs is in part distributed to the organ which secretes the lithic acid (saccus calcareus), and is then collected again to be sent to the auricle.

Cephalopoda.—In the sepia (fig. 4) there are three separate ventricles; the systemic ventricle or heart gives off the aorta, which distributes the blood to the body, from which it is brought by veins to the two lateral branchial hearts; by these it is sent to the branchiæ, and by the branchial veins is returned to the systemic heart.

In *fishes* (fig. 5) there is but one auricle and one ventricle, the venous

Fig. 4.†

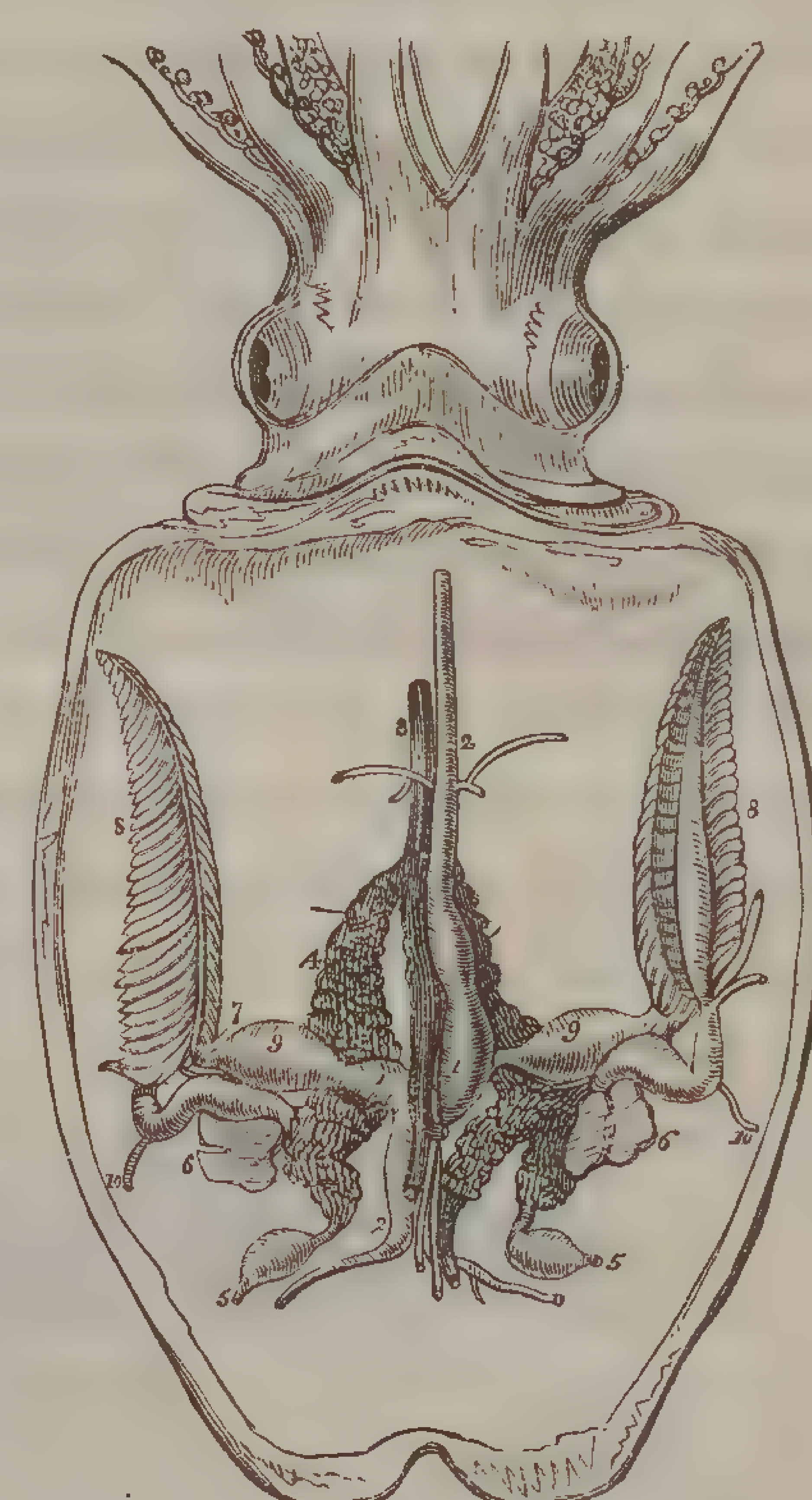
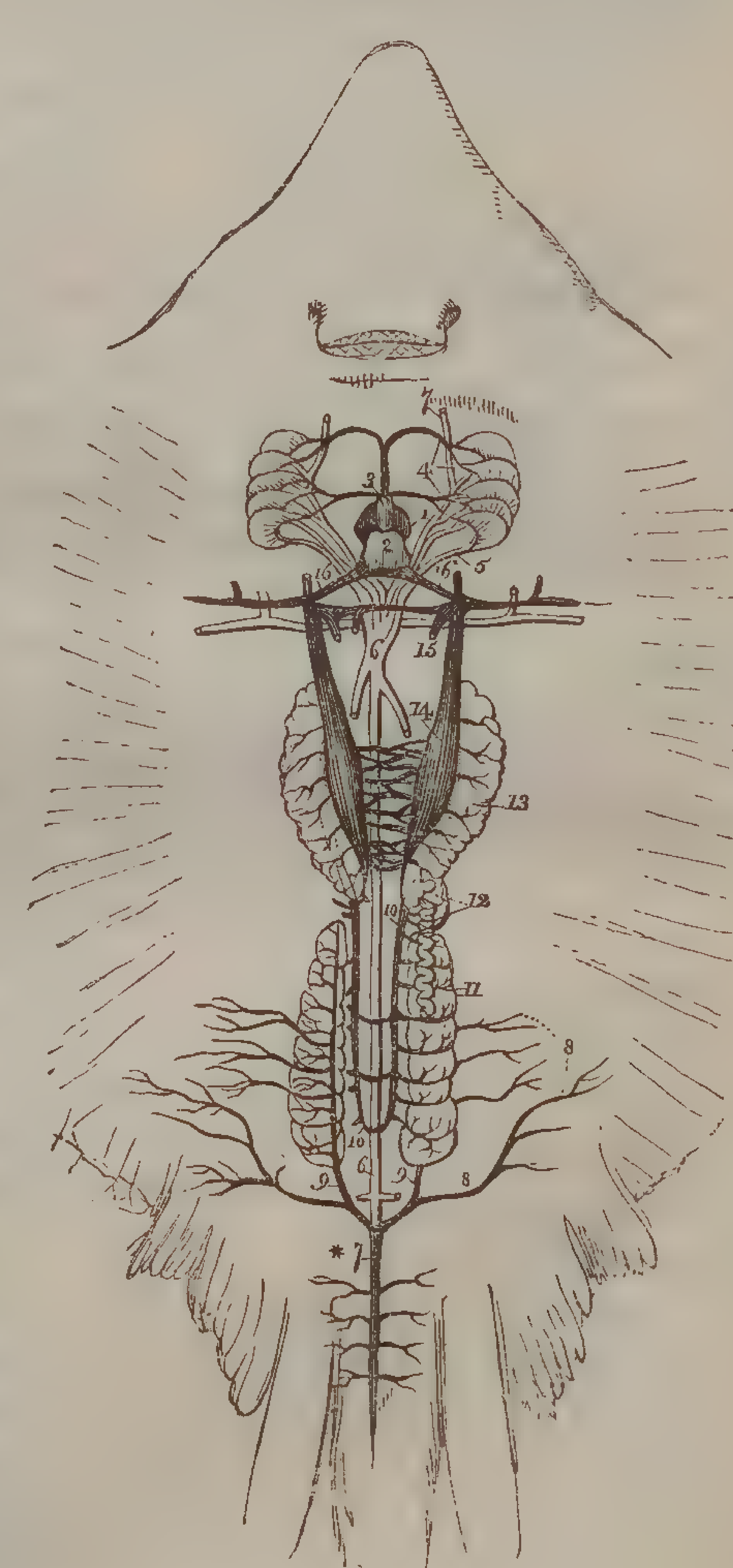


Fig. 5.‡



* Erschein. u. Gesetze des organ. Lebens, i. p. 227.

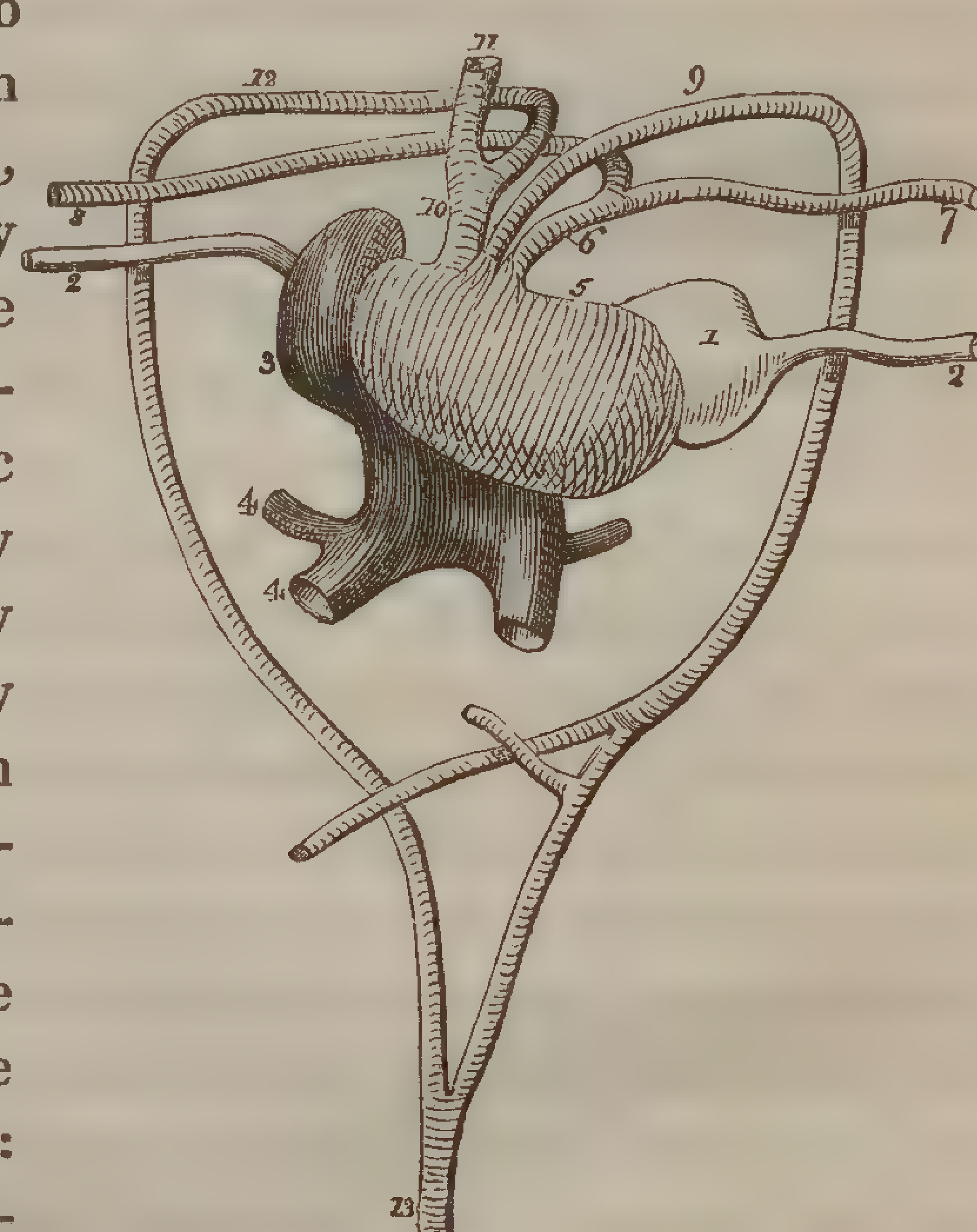
† [Circulation in the sepia officinalis or cuttle-fish, after Hunter. Catalogue of Mus. of Coll. of Surgeons, vol. ii.—1. The systemic ventricle; 2. the systemic arteries; 3. vena cava, with its spongy cellular covering; 4, 4. the divisions of the cava going to the branchial ventricles (6, 6), which likewise receive the blood from the visceral veins (5, 5), and from the great veins of the mantle, of which 10 is one, the others are those which are seen running up by the side of the branchia (8); 7. branchial artery; 9, 9. branchial veins.]

‡ [Diagram of the circulation in the skate, raia batis.—1. The auricle; 2. the ventricle; 3. the bulbus arteriosus; 4. the branchial arteries; 5. the branchial veins; 6. the aorta; 7. an artery given off by a branchial vein to the head (there are two or three such arteries on each side). The venous system commences by the single caudal vein (7*), which divides into two branches (9, 9), one going to the posterior surface of each kidney (11), to which it is distributed after

blood from the body generally being collected in the auricle and thence transmitted to the ventricle. From the ventricle it is impelled into the contractile bulbus arteriosus, which gives off the arteries for the branchiæ, generally four on each side; from the branchiæ the blood is returned by the same number of branchial veins which unite to form the aorta, by the branches of which it is distributed to the body.

[In *reptiles* (fig. 6) there are two auricles and one ventricle imperfectly divided into two cavities. The venous blood brought from the body to the right auricle is partially mixed in the ventricle with arterialised blood, which is received from the lungs by the left auricle, and poured into the ventricle: from the right compartment of the ventricle the left aortic trunk and the left pulmonary artery generally arise; from the left cavity the right aortic trunk and generally the right pulmonary artery; it is from the right aortic trunk that the arteries of the head and upper extremities arise, and these parts, as in the fœtus of mammalia and birds, receive a larger proportion of arterial blood: the two arterial trunks unite posteriorly to form the descending aorta.

Fig. 6.*



In the heart of the crocodilus lucius (fig. 7), of which an excellent description has been recently published by Dr. Bischoff of Heidelberg,† the septum between the ventricular cavities is complete, but there is a communication between the two aortic trunks immediately above their

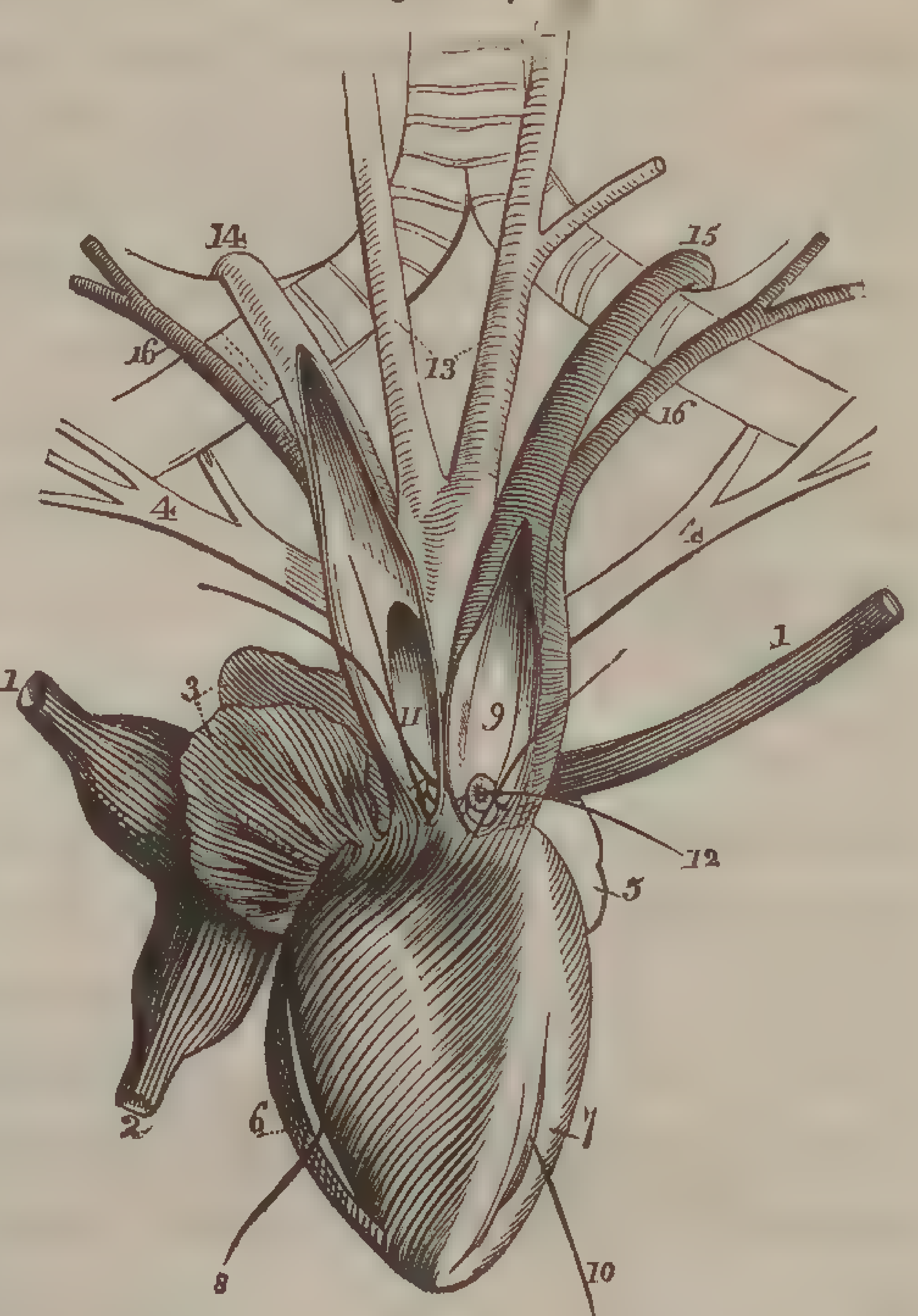
receiving veins from the muscles of the back. The two venæ (10) cavæ commence by a series of loops or arches, receive the renal veins (which are seen on the left side running between the lobes of the kidney), and afterwards the veins of the epididymis and vas deferens, and then, running up behind the testes (13), unite with the large sinuses (14) which lie at the inner border of these organs. The sinuses mentioned communicate very freely with each other. At the point where the cava on each side pierces the diaphragm it is joined by the brachial and jugular veins, and by the hepatic veins (15), of which there are three communicating by a cross branch. Within the pericardium the venæ cavæ unite, forming a transverse tube, from which there is one opening into the auricle.]

* [Heart of turtle, after Martin St. Ange.—1. Left auricle; 2, 2. the pulmonary veins; 3. the right auricle; 4, 4. systemic veins; 5. the ventricle; the common trunk (6) of the pulmonary arteries, and the left aortic trunk, arise from the right side of the heart; the trunk (10), which gives off the right aortic trunk (12) and the great artery (11) of the head, arises from the left side of the heart; 13. the aorta.]

† In Müller's Archiv. for 1836.

origin, by means of an opening through which, during the diastole of the ventricles, blood might pass from one aortic trunk to the other, but not during the systole, it being then closed by the valves of the aortic orifices.]

Fig. 7.†



Amphibia.—Intermediate in the chain of animals between fishes and reptiles is the class of amphibia or batrachian reptiles, of great interest in a physiological point of view on account of the metamorphosis of the branchial into the pulmonary circulation which is observed in them. All the amphibia have two auricles,* the separation between which is not visible externally, and one ventricle; they have two occipital condyles, no cochlea in the ear, no fenestra rotunda, no penis, no true ribs. All the true reptiles (saurians, chelonians, and ophidians) have two auricles distinctly separate even on the exterior, one ventricle, one occipital condyle, a cochlea and fenestra rotunda, true ribs, a distinct penis, and they undergo no metamorphosis. All the amphibia appear to have branchiæ in the early stage of their existence, but all except the proteidea lose them at a later period. The distinction between the two classes—reptiles and amphibia—is therefore sufficiently obvious.‡

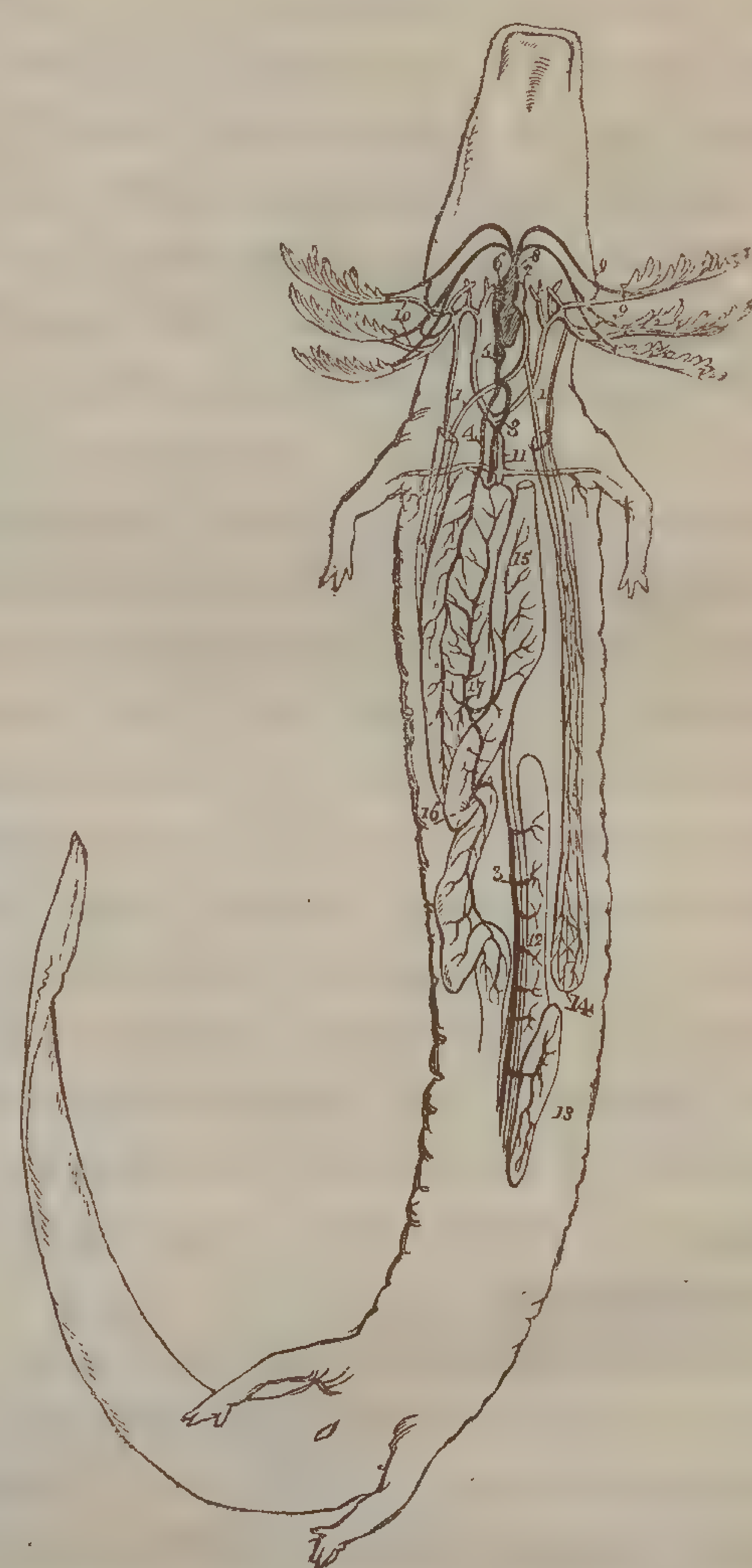
* [The existence of two auricles in the perenni-branchiate amphibia was discovered by Mr. Owen, (See Transactions of the Zoological Society for 1834), and a year later by Prof. Mayer of Bonn. See his Analect. zur vergl. Anat. 1835.]

† [Heart of crocodilus lucius, after Dr. Bischoff.—The venous blood brought by the superior venæ cavæ (1, 1), and by the inferior cava (2), to the right auricle (3), is poured into the right ventricle (6). The arterial blood is transmitted through the pulmonary veins (4, 4) to the left auricle (5), and thence to the left ventricle (7). The wire (8) shows the course of the venous blood to the arterial trunk (9), which gives off the pulmonary arteries (16, 16) and the left aortic arch (15). The wire (10) indicates the course of the arterial blood to the arterial trunk (11,) from which arise the carotid arteries (13), and the right aortic arch (14.) Besides the opening between the two great arterial trunks, through which the wire (12) is passed, there is a communicating branch passing from the right aortic arch to the left, which is continued to the posterior extremities, while the right is distributed to the abdominal viscera. The similarity between the course of the circulation in this reptile to the fœtus of mammalia and birds, and the analogy pointed out by Professor Mayer to exist between the left aortic arch of the crocodile and the ductus arteriosus, are very striking.]

‡ The amphibia may be arranged in five orders, (as follows.)—I. Cæciliæ, without feet and tail, vermiform.—In the first period of their existence they have a branchial cavity, in which there are two branchial clefts on each side of the neck, which I have discovered in the cæcilia hypocyanea ; at a later period they have lungs without bran-

In the *proteidea*,—for example, the proteus, (fig. 8,)—the arterial trunk

Fig. 8.*



chiæ or branchial foramina. Their os hyoides has four pairs of arches, in the larvæ five.—[This is the order apoda of Mr. T. Bell.—See Cyclop. of Anat.]

2. Derotremata.—The individuals of this order have extremities and caudal prolongation, an opening on each side of the neck without true external or internal branchiæ. They breathe by means of lungs; have four feet. The genera are the amphiuma and menopoma.—[The abranchia of Mr. Bell.]

3. Proteidea. — These have extremities and caudal prolongation, and both lungs and branchial clefts on each side of the neck, with external tufted branchiæ throughout life. The genera are siren, menobranchus, proteus, axolotes.—[Amphipneurta of Mr. Bell.]

4. Salamandrina.—During the first period of their larval condition the salamandrina have external branchiæ and branchial clefts, no extremities, but a caudal prolongation. In the second period of their existence, they have, besides a tail, four extremities, of which the anterior appear first; at the same time they have tufted branchiæ, and branchial clefts, with rudiments of lungs. In this stage of their developement therefore they resemble the permanent state of the proteidea. In the perfect state they retain the tail; but their branchiæ and branchial clefts disappear when the larval state ceases.—[The urodela of Mr. T. Bell.]

5. Batrachia.—The frogs and toads [anoura of Mr. Bell].—These in the first stadium of their larval condition have a tail and no extremities, and have branchial clefts and arches, and external tufted branchiæ. In the second period they lose their external branchiæ, but have internal branchiæ on the branchial arches, the branchiæ being covered by a membrane which leaves but one opening on the left side in the frog; they have still a tail and no extremities. In the metamorphosis from the larval condition they acquire extremities of which the posterior appear first, they lose their branchiæ, and their tail also wholly disappears by absorption.

During the larval state of frogs and salamanders, both articulating surfaces of the bodies of the vertebræ are excavated conically, as in fishes; in the cæciliæ, derotremata, and proteidea this state is persistent.—See J. Mueller in Tiedemann's Zeitschrift für Physiol. iv. 2. On the heart of the amphibia consult M. Weber, Beiträge zur Anat. ū Physiol. Bonn, 1832.

* [Circulation in the proteus anguinus, after Rusconi.—1, 1. The pulmonary veins; 2. left auricle; 3. vena cava; 4. hepatic vein; 5. sinus venosus; 6. right auricle; 7. the ventricle; 8. the bulbus arteriosus; 9. branchial arteries; 10. branchial veins. Between the branchial arteries and veins communicating branches are seen which complete the arches. 11. Descending aorta. From the united trunk of the second and third bran-

divides immediately into several aortic arches on each side, corresponding to the branchial arches; the aortic arches unite again posteriorly, forming the aorta abdominalis. From the aortic arches the great branchial arteries arise, and the branchial veins terminate in them.

In the salamander.—In the larva of the salamander the arterial trunk divides, as in the proteus, chiefly into the branchial arteries which give off anastomosing branches to the branchial veins: the branchial veins by their union form the main stem of the general arterial system. During the metamorphosis from the larval state, the circulation in the branchiæ gradually ceases and becomes limited to the permanent aortic arches.*

Fig. 9.†

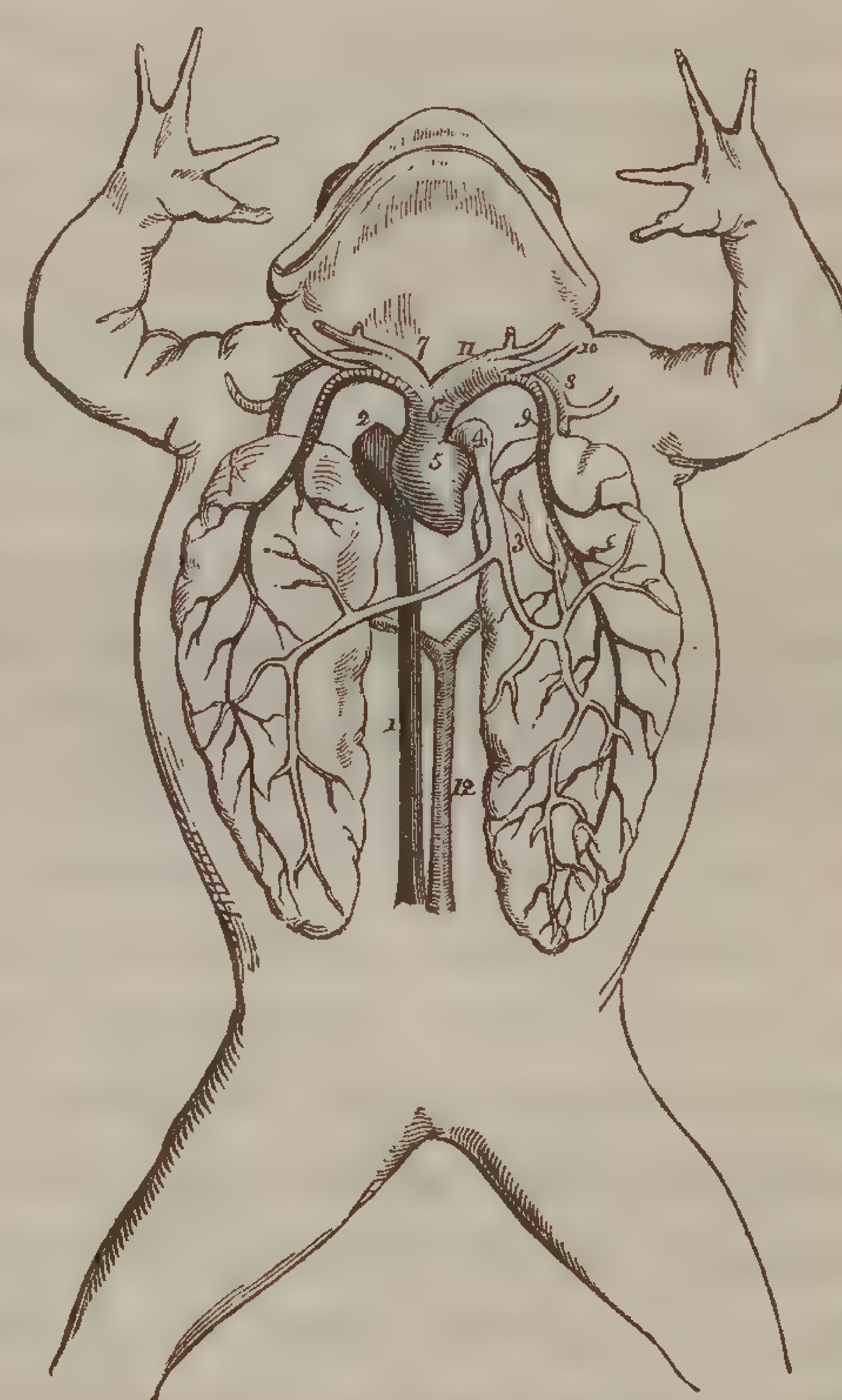
In the frog.—The branchial circulation in the frog, during the earliest period of its larval condition, when it has external branchiæ, is similar to that in the larva of the salamander. During the second period (fig. 9), in which it has internal covered branchiæ, and in which the lungs begin to be developed, the distribution of the vessels is, according to Huschke, more like that of fishes; the arterial trunk divides into the branchial arteries for the four branchial arches, the branchial veins collecting into large trunks run parallel to the arteries. In the larvæ of the frog, however, there is a short anastomosing branch connecting the artery and vein at the commencement of each branchial arch, which does not exist in the fish. After the metamorphosis (see fig. 10) there remains on each side but one arterial arch, which unites with the one of the opposite side to form the aorta abdominalis, and which gives off posteriorly the arteria brachialis. The pulmonary arteries and those of the head, although they appear to arise from the commencement of these two aortic arches, do not really do so; for, when accurately examined, each of the two diverging stems into which the bulbus arteri-

chial vein the pulmonary artery arises, and descends to the lung (14); 12. kidney; 13. testicle; 15. stomach; 16. intestine; 17. vena porta ramifying in the liver.]

* Rusconi, Amours des salamandres. Milan, 1821.

† [Diagram of circulation in the tadpole in its second stage.—1. The vena cava; 2. the right auricle; 3. the pulmonary veins; 4. the left auricle; 5. the ventricle; 6. bulbus arteriosus; 7. branchial arteries; 8. branchial veins; 9. aorta; 10. pulmonary artery arising from fourth branchial arch.]

Fig. 10.†



osus divides, is found to consist of three trunks united, the cavities of which, however, are separated by thin septa merely. These are the remains of the branchial arteries which have united to form apparently one stem. The middle one of these vessels is continuous with the aorta. The most inferior gives off the pulmonary artery and a vessel to the occiput, while the superior one forms the arterial trunk from which the head is supplied. Near the origin of the arteries of the head there is a glandular enlargement,—the so-called carotid gland. This gland is formed of minute ramifications of the entering vessels, which again unite into a single trunk that issues from the mass.* This body is supposed to be the remains of the capillary vessels of the first branchial arch. I have satisfied myself that it has a cavity in its interior, and that the stem entering it is continuous till its exit, passing through a spongy tissue, which is most dense internally, although the external surface when finely injected does present a delicate network, as Huschke describes, formed from vessels passing in and out.

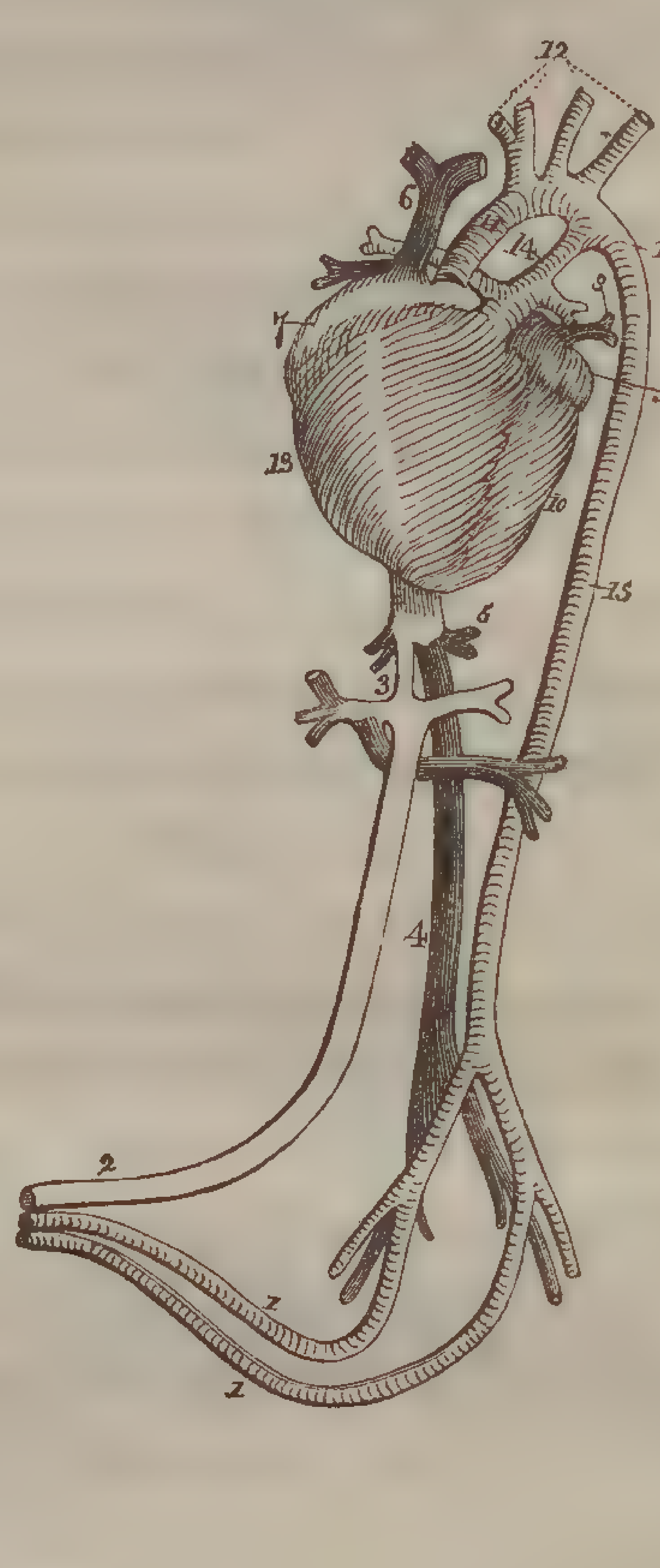
Aortic arches in the embryo of higher vertebrata.—The true reptiles never possess branchiæ, and undergo metamorphosis only during the fœtal state, like the other vertebrata. In the earliest period of fœtal life, the embryos of all vertebrate animals have clefts in the neck, and, between these, arched plates. In these plates run the aortic arches, which unite again posteriorly into one common trunk. This was discovered by Rathke; it is satisfactorily seen in the embryo of the bird on the third day of incubation. A similar structure, but less distinct, exists also in mammalia and in man. It is more easily seen in the embryo of reptiles. In these higher vertebrata there are no real branchiæ with branchial lamellæ, but merely branchial arches, from which in fishes and amphibia the branchiæ are developed by ramification of the aortic arches,

* This was shown by Huschke. Zeitschrift für Physiol. iv. 1.

† [Diagram of circulation in the frog.—1. The vena cava ; 2. the right auricle ; 3. pulmonary vein ; 4. left auricle ; 5. ventricle ; 6. bulbus arteriosus, which divides into two branches (7) ; the division of these branches into three branches by internal septa is indicated by dotted lines ; 8. aortic arch giving off brachial artery ; 9. pulmonary artery ; 10. a branch to the occiput ; 11. carotid ; 12. descending aorta.]

but which in all other vertebrate classes gradually disappear; being, it would seem, converted into the cornua of the os hyoides.* In all vertebrate animals then, during the earliest stage of existence, the main arterial stem divides into aortic arches. These arches are indeed persistent in reptiles; in some cases two on each side,—as in the true lizards and blind worms;—in other cases one only on each side,—as in serpents. In the higher vertebrata, birds, and mammalia, in which there are two auricles and two ventricles, it is during the fœtal state only that there are several aortic arches; at first, indeed, several on each side, which unite posteriorly to form the descending aorta. In birds the most anterior of the three arches gives off the vessels for the anterior part of the body; the most posterior, the pulmonary artery: at a later stage of developement, and throughout fœtal life, there are two arches from the right ventricle, from which the pulmonary arteries are given off; and one arterial stem from the left ventricle, which gives origin to the vessels of the anterior part of the body, and forms the arch of the aorta. After the bird has escaped from the shell, the pulmonary arteries also become independent, from the anastomoses between the arterial arches that arise from the right ventricle, with the aortic arch from the left ventricle, ceasing to exist.‡ In mammalia there are during fœtal life two aortic arches, which unite posteriorly to form the descending aorta (see fig. 11). Of these, one arises from the left ventricle, and gives off the arteries for the upper part of the body; the other from the right ventricle gives off the pulmonary arteries as lateral branches. The

Fig. 11.†



* J. Müller, Meckel's Archiv. 1830, p. 419.

† [Diagram of the circulation in the human fœtus. 1, 1. Umbilical arteries; 2. umbilical vein. The blood of the umbilical vein is partly distributed to the liver, in the right lobe of which it becomes mixed with the blood of the porta; in part it passes directly by the ductus venosus (3), to the vena cava inferior (4). 5. Hepatic veins; 6. superior cava; 7. right auricle; 8. pulmonary veins; 9. left auricle; 10. left ventricle; 11. ascending aorta or left aortic arch; 12. vessels to the head and upper extremities; 13. right ventricle; 14. ductus arteriosus, or right aortic arch; 15. descending aorta.]

‡ S. Huschke, Isis, 1828. 160.

continuation of this latter arch, namely, the ductus arteriosus, by which it unites with the aortic arch, at last ceases to be pervious, and then the pulmonary arteries become the sole branches of the trunk arising from the right ventricle. The arch of the aorta, or arcus ventriculi sinistri, in mammalia, turns from the left side behind the œsophagus, while in birds it turns from the right side; when it is recollected that in the embryo state of both classes of animals there are several arterial arches on each side, this apparent anomaly becomes easily intelligible. Besides the communication between the two arterial arches, there is in the fœtus another means of communication between the two sides of the heart, namely, the foramen ovale. When either this opening, or the ductus arteriosus, remains unclosed after birth, the arterial and the venous blood are mixed, and the cœrulean disease is produced.

Varieties in the circulation dependent on the relation of the lesser and greater circulation.—As soon as a true circulation is met with in ascending the animal scale, all further modifications depend on the relation in which the vessels of the respiratory organs, or the lesser circulation, stand to the vessels of the body, or greater circulation. Thus either a portion only of the blood is aerated in the course of the greater or systemic circulation, in which case the lesser circulation, to use Cuvier's expression, is merely a fraction of the greater, or all the blood must first pass through the lesser circulation of the lungs or branchiæ, before it is distributed to the body generally.

The varieties which nature presents in the origin of the arteries and veins of the respiratory organs from the systemic circulation are very numerous, and seem indeed to comprehend all imaginable forms. They may be arranged as follow:

A. The lesser circulation a fraction of the greater circulation.

1. The lesser circulation a part of the venous system: example, in the conchifera, if Bojanus is correct, a portion of the venous blood returns immediately to the auricles, while the greater part previously traverses the branchiæ.

2. The lesser circulation a part of the arterial system: example, in the proteidea, and in the frogs and salamanders during the larval condition, the aortic arches give off the branchial arteries and receive the branchial veins as lateral branches.

3. The lesser circulation forming a part of the arterial and venous systems: example, *a*, The salamander and frog in their perfect state have no longer branchiæ, the proteidea retain both branchiæ and lungs throughout their existence; in both, the pulmonary arteries are branches of the aortic arches, and the pulmonary veins terminate in the left auricle, the veins of the body in the right auricle, as has been discovered by Dr. J. Davy, Martin St. Ange and M. Weber. *b*, In the true reptiles, the pulmonary artery arises from the main arterial trunk, or

from the ventricle itself with the arteries for the body; the branchial veins empty themselves into the left auricle, the veins of the body into the right auricle.

B. The lesser circulation opposed to, or distinct from, the greater circulation.

1. The lesser circulation commencing in the veins of the body and terminating in the heart: example, the mollusca and higher crustacea.

2. The lesser circulation commencing in the branchial arteries which arise from the great arterial stem, or bulbus aortæ, and returning by the branchial veins to a new arterial stem for the rest of the body: example, fishes.

3. The lesser circulation arising from the pulmonary ventricle and returning to the ventricle of the systemic circulation: *a*, In the sepia, the aortic heart and the two branchial hearts are separate and without auricles: *b*, In birds and mammalia there is one pulmonary and one aortic ventricle, each with an auricle, united to form one heart: the pulmonary veins open into the auricle of the left or aortic ventricle; the veins of the body,—the venæ cavæ,—into the auricle of the right or pulmonary ventricle.

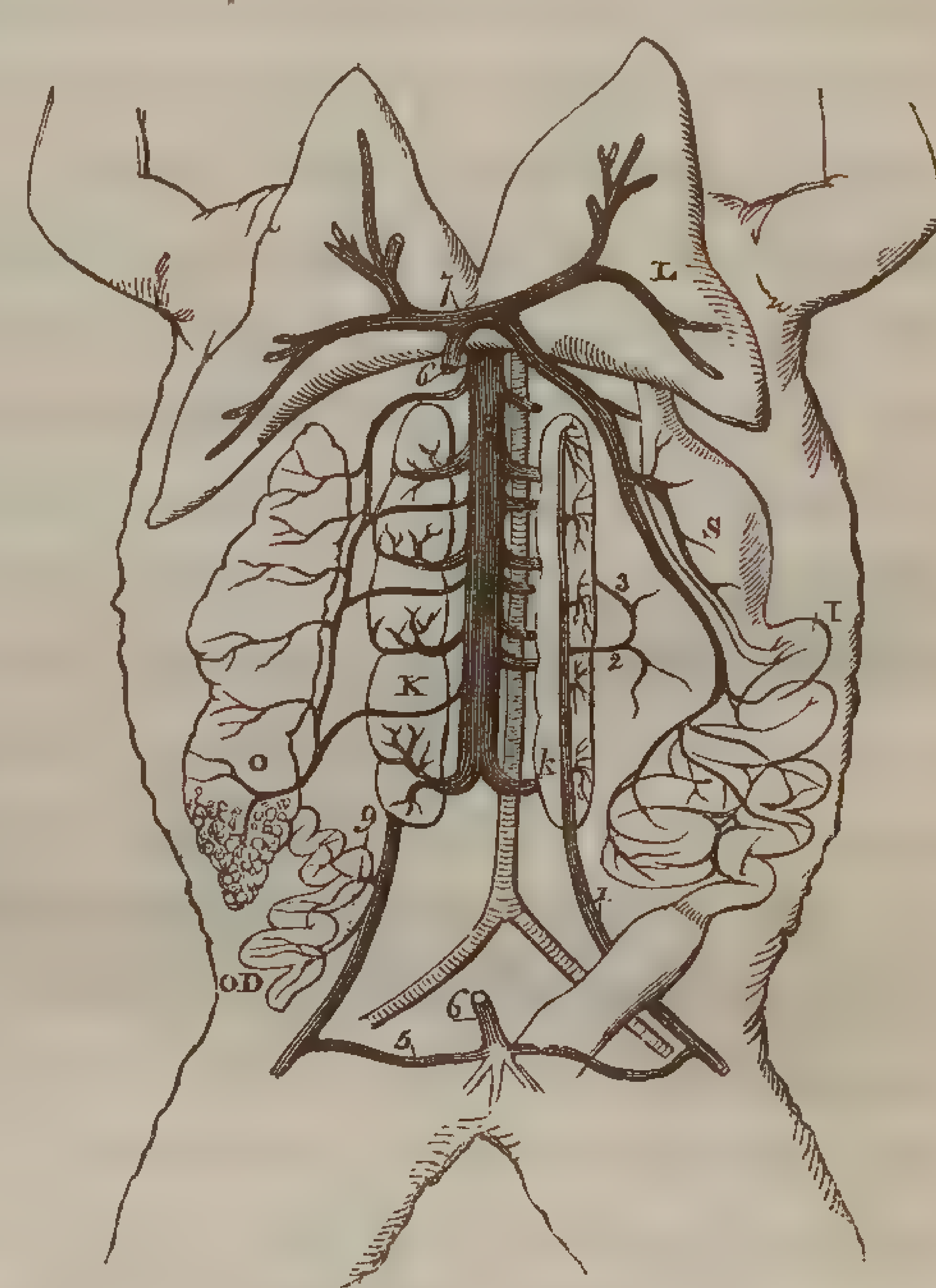
So that as regards the relation which the pulmonic or branchial circulation bears to the systemic circulation, reptiles and amphibia would appear to be inferior in the scale of organisation to fishes, to the majority of mollusca, and to crustacea. But Cuvier rightly observes, that respiration in water is much more imperfect than when performed in the air, and consequently that the imperfect respiration of the mollusca, crustacea, and fishes in the water, although all their blood passes through the respiratory organs, does not differ in result from the more perfect pulmonary respiration of reptiles, in which the lesser circulation is only a fraction of the systemic circulation. Still those gasteropoda which respire by means of pulmonary sacs would appear to be higher in the scale than the reptiles with a similar mode of respiration, inasmuch as a part only of the blood in the latter, in the former all the blood, is aerated before it enters the general circulation. But it must be remembered that in the lungs of the gasteropoda the number of the vessels and their ramification, and consequently the exposure of the blood to the air, are much less considerable than in the lungs of reptiles.

The larvæ of the amphibia respire by means of branchiæ in the water; and since in that condition a portion only, although a large portion of the blood, is aerated before it enters the systemic circulation, these animals are in this respect certainly inferior to fishes. But we have already seen that this arrangement in the larvæ of the amphibia is necessary in order that the pulmonary circulation may afterwards be developed from the previous branchial circulation.

Portal circulation.—Besides the lesser or pulmonary circulation, there is in all vertebrate animals another still smaller circulation, which, like the branchial circulation of amphibia, is a "fraction" merely of the general circulation. This is the portal circulation; it is a mere subordinate part of the venous circulation, in which the blood makes an additional circuit before it joins the rest of the venous blood. There are in the vertebrate classes two portal circulations; one of the liver, the other of the kidneys (fig. 12). The latter exists only in reptiles, amphibia, and fishes; the former in all the vertebrata.

In mammalia, including man, the veins which collect the blood from the spleen, stomach, intestines, gall-bladder, and pancreas, unite to form the portal vein, which ramifies through the liver like an artery: from the capillary vessels of the liver, the blood, a part of which was supplied by the hepatic artery, returns through the hepatic veins to the vena cava, in which it becomes mingled with the venous blood of other parts. In the other classes of the vertebrata, a part of the blood of the lower extremities also is carried to the portal vein; and in fishes sometimes the blood from the air-bladder and genital organs.†

Fig. 12.*



In reptiles and amphibia, the kidneys have, besides the renal arteries, portal veins (fig. 12, 1), which bring to them a part of the blood of the posterior extremities, and of the tail. In these animals the blood returned from the posterior extremities, from the abdominal muscles, and from the tail, goes partly to the liver, and partly to the kidneys; in frogs and salamanders to these viscera only; while in some reptiles, as the crocodile, a portion of it is sent to the vena cava. In some fishes, for

* [Venous circulation in the toad.—1. Afferent renal vein ramifying on the posterior surface of the kidney (k); 2. vein from the muscles of the back joining the afferent renal vein; 3. a branch coming from the interior of the spinal canal; 5. communicating branch between the ischiadic, or afferent renal, and the anterior abdominal vein (6), which runs over the surface of the abdomen and terminates in the vena portæ (7), which is formed chiefly by the veins of the stomach (S) and intestines (I); 8. the vena cava formed principally by the efferent renal veins, which run on the anterior surface of the kidney (K). The veins of the ovaries (O), also pour their blood into the cava, while the veins (9) of the oviduct (OD), join the afferent vein of the kidney.]

† See Jacobson, Nicolai, and Rathke.

example, the gadus, the blood of the tail and middle part of the body goes wholly to the kidneys (see fig. 5); in others, the venous blood of the posterior parts of the body is distributed to the kidneys, liver, and vena cava, as is the case in the carp, pike, and perch.*

Meckel, who considers these portal veins which carry blood to the kidneys to be ordinary venous trunks conveying it from them, founds his opinion chiefly on the class of birds, in which Jacobson incorrectly described portal veins going to the kidneys; but the non-existence of these veins in birds, which had been previously proved by Nicolai, is no argument for their not existing in reptiles, amphibia, and fishes, in which classes indeed Nicolai has established their presence.

Essential characters of the heart.—The principal impelling power of the circulation is the rhythmic motion of the heart. The heart is that part of the vascular system which, from having muscular parietes, which the blood-vessels do not generally possess, is endowed with contractility. In its simplest form, therefore, the heart still resembles a vessel; this is exemplified by the vessel-like multiple hearts which constitute at the same time the main vascular trunks of the annelides, by the contractile vascular trunks on the intestinal canal of the holothuria, and by the dorsal vessel of insects, which is divided into a series of chambers. The correctness of this view is very evident on examining the organ in different orders of the crustacea: thus, in the squillæ the heart is a contractile dorsal vessel, while in the decapoda it presents one short and circumscribed chamber or ventricle.

In the embryo of the higher animals the heart is at first tubular, and is nothing more than the contractile part of the vessels at which the venous trunks are reflected into the arterial stem.

In the adult too of the higher animals the heart consists of a short double muscular sac, but the contractile substance is continued for a certain extent on the venous trunks that open into it, and in fishes and reptiles, upon a part of the arterial stem,—the so-called bulbus aortæ. In the frog the trunks of the venæ cavæ can be most distinctly seen to contract regularly like the heart. This was observed by Haller,† Spallanzani, and Wedemeyer. The contraction appears to me to extend on the inferior cava as far as the liver; and is still continued, and with regularity, in the venous stems, after the heart is removed. First, the cavæ contract, then the auricles, next the ventricles, and lastly the bulbus aortæ. I have observed contraction of the great veins in the mammalia, both in the young marten and in the young cat; in these animals, however, the contraction of the venæ cavæ and pulmonary veins is synchronous with the contraction of the auricles.

* Jacobson, Meckel's Archiv. 1817. 147. Nicolai, Isis, 1826. 404.

† Elementa Physiol. t. i. 125.

In young animals the most distinct contractions of the pulmonary veins are perceptible as far as these vessels can be followed in the substance of the lungs. The contraction of the cardiac end of the superior vena cava is as distinct. But, during the contraction, the distance to which the contractile substance of the cavæ extends may be distinguished; beyond this limit the vena cava exhibits not the slightest contraction, but becomes rather turgid and distended by blood at the time that the parts of the vessel contiguous to the right auricle are contracted. At the origin of the vena cava of serpents Retzius has described a layer of peculiar fibres, and E. H. Weber has found the same in the inferior cava of mammalia.

These observations indicate, that in its simplest form the heart is merely that part of the vascular system which is furnished with muscular structure, and endued with the power of active motion; and that it is still the heart when, as in the lower animals, it has the form of a simple contractile vascular stem. The rest of the vascular system consists merely of tubular canals, which, in reference to motion, are passive, but may exert other important influences on the blood. Thus, for example, by virtue of a power, the nature of which is not known, they maintain the fluidity of the blood as long as it is in motion; and the interchange of matters between the blood and the tissues which takes place through their parietes is effected by their influence.*

CHAPTER II.

OF THE GENERAL PHENOMENA OF THE CIRCULATION.

The heart of adult man in the middle period of life contracts seventy to seventy-five times in a minute; the frequency of its action gradually diminishes from the commencement to the end of life, thus:

In the embryo the number of beats in a minute is	150
Just after birth	from 130 to 140
During the first year	115 to 130
During the second year	100 to 115
During the third year	90 to 100
About the seventh year	85 to 90
About the fourteenth year	80 to 85
In the middle period of life	70 to 75
In old age	50 to 65

In persons of sanguine temperament the heart beats somewhat more frequently than in those of the phlegmatic; and in the female sex more frequently than in the male. The number of the pulsations in a minute varies very much in different animals.

* I have given a more elaborate description of the various forms presented by the circulation in the animal kingdom, in Burdach's Physiologie, B. iv.

In fishes the number of beats in a minute is	from 20 to 24
In the frog	about 60
In birds	from 100 to 140
In rabbits	about 120
In the cat	110
„ dog	95
„ sheep	75
„ horse	40

After a meal the heart's action is accelerated, and still more so during bodily exertion; it is slower during sleep. According to Parrot,* the frequency of the pulse increases in a corresponding ratio with the elevation above the sea:

When the pulse at the level of the sea was	70
At 1000 metres † above its level, it was	75
1500	82
2000	90
2500	95
3000	100
4000	110

In inflammations and fevers the pulse is much more frequent than during health. When the vital powers decline, it becomes frequent and feeble. In nervous affections with more oppression than exhaustion of the forces, the pulse is often remarkably slow.

If the heart of a living mammiferous animal or bird is laid bare, the two ventricles are seen to contract simultaneously; the two auricles with the commencement of the pulmonary veins and of the venæ cavæ also contract simultaneously, the contraction of the auricles and that of the ventricles not being synchronous. In warm-blooded animals the auricles contract immediately before the ventricle. In the frog the contractions of the venous trunks, of the auricles, the ventricle, and the bulbus aortæ appeared to me to follow the order in which I have named the parts, the intervals between the four contractions being nearly equal; so that the same interval of time elapsed from the contraction of the auricles to the contraction of the ventricle, as between the contraction of the ventricle and that of the bulb of the aorta. I am convinced, from repeated observations, that the auricles and ventricle do not, as Oesterreicher ‡ asserts, alternate in action at equal intervals like the motions of the pendulum, but that the time that intervenes between the contraction of the auricles and the contraction of the ventricle is much less than that which elapses from the moment of the contractions of the ventricle to the moment when the auricles again act; and that generally the contraction of the bulbus aortæ and

* Froriep's Notizen, 212. See also Niek, über die Bedingungen der Hanfigkeit des Pulsus. Tübingen, 1826.

† [A metre is about three feet three inches.]

‡ Lehre vom Kreislauf des Blutes. Nürnb. 1826.

venous trunks occur in the interval of time last indicated. In warm-blooded animals I have seen the contractions of the auricle cease altogether for some moments, which must have been caused by the injury inflicted in making the observation. Under ordinary circumstances, the auricular contraction was always a very quick motion immediately preceding the action of the ventricle, so that the interval of time from the contraction of the auricles to the contraction of the ventricle is at any rate very much shorter than the interval between the contraction of the ventricles and that of the auricles.

The contraction (systole) only of the heart is an active state; the dilatation (diastole) is the moment of repose, in which the fibres are relaxed, and in which the blood is poured from the contiguous veins into the cavities of the heart, to fill the vacuum consequent on the relaxation of its fibres; the valves of the heart being so arranged as to allow the influx of the blood from the veins. The dilatation of the heart was supposed by Bichat, and some other French physiologists, to be an active movement, but Oesterreicher* has by a very ingenious experiment refuted this supposition. He removed the heart of a frog from the body, and laid upon it a substance sufficiently heavy to press it flat, and yet so small as not to conceal the heart from view; he then observed that during the contraction of the heart the weight was raised, but that during dilatation the heart remained flat. This experiment shows that the dilatation of the heart is not a muscular act; at the same time, however, it must be recollected that the walls of the heart during life cannot become so relaxed at the time of the diastole, as in a heart removed from the body, even although the cavities of the heart were not filled with blood; for during life the capillary vessels of its substance are at the time of relaxation injected with blood, which during the contraction is pressed out of them, and this filling of its vessels must give it some degree of firmness and rigidity.

The contraction of the ventricles of the heart would drive the blood into the auricles and veins, as well as into the arteries, if the valves were not so constructed and attached as to allow the expulsion of the blood only in certain directions. There are certainly no valves to prevent the auricles from forcing the blood into the veins; but the stream of venous blood towards the heart checks its regurgitation in this direction, while its passage from the auricle into the ventricle is free, for the valve at the auriculo-ventricular orifice is so attached that it allows the blood to flow into the ventricle; but, when the ventricle contracts, the same valve prevents the regurgitation of the blood into the auricle, being by the pressure of the blood spread out so as to close the orifice. The escape of the blood from the ventricle into the great arteries is unimpeded, the pouch-shaped semilunar

* Loc. cit. p. 33.

valves situated at the arterial orifice of the ventricle being separated from each other, and laid close to the walls of the artery by the stream of blood forced into it. And when the contraction of the ventricle ceases, regurgitation from the arteries cannot take place, for the blood itself presses down the valves towards the centre of the vessel, and spreads them out so as to close the arterial orifices of the ventricles. The heart by this arrangement of the valves is constituted a kind of forcing-pump, like the common syringe with two valves, of which one admits the fluid on raising the piston, but is closed again when the piston is forced down, while the other opens for the escape of the water, but closes when the piston is raised, so as to prevent the regurgitation of the fluid already forced through it.

The vascular system must be regarded as being constantly filled with blood in all parts. The heart's cavities alone contract at each beat so as to expel nearly all their contents; but several observations show that even the ventricles do not empty themselves completely during their contraction. The vessels, on the other hand, from the commencement of the arteries to the capillary vessels, and thence to the insertion of the venous trunks into the heart, are filled with blood, both during the contraction of the ventricles and at the time of their relaxation; neither air nor a vacuum exists in any part of the vascular system. So that the contraction of the aortic or left ventricle cannot advance the blood in the arteries except by forcing on the column of blood already contained in them; and the advance of the column is proportionate to the space which the blood forced through the aortic orifice by each contraction of the ventricle—namely, from one to two ounces—occupies in the commencement of the aorta. When the contraction of the ventricle remits, the cause of the motion ceases, but the elasticity of the arteries overcomes the resistance offered by friction in the minute vessels, and still forces the blood onwards; a continuous current is thus produced from the aortic valves to the capillary vessels; when the aortic ventricle again contracts, and again forces one or two ounces of blood into the aorta, the current is accelerated, and the column of blood is advanced to the same extent as before. The result of this succession of actions must be, that exactly the same quantity of blood enters the heart from the veins as was expelled from it in the same space of time by the contraction of the ventricles; for the whole mass of blood forms one great circle from the heart to the heart,—a circle, at each and every point of which the same quantity of blood must pass within a given time. By their contraction the ventricles are never completely emptied, for, when the contraction ceases, the blood impelled by the *vis à tergo* immediately flows from the veins and auricles into the ventricles to fill the impending vacuum; it is the same with the auricles.

The pressure of the column of blood against the elastic walls of the arteries at every contraction of the ventricle produces what is called the pulse. The phenomenon will be more particularly considered at a future page; here it is only necessary to remark, that the sensible pulse of the arteries is synchronous, or nearly so, with the contraction of the ventricle; the arterial pulse is somewhat later than the heart's beat, but the difference of time is scarcely perceptible. In the capillaries and veins the pulse is not detectible.

The impulse of the heart, pulsis cordis, must not be confounded with the arterial pulse. The heart's impulse is the shock communicated by the apex of the heart to the walls of the thorax in the neighbourhood of the fifth and sixth rib. But it is not at present known whether it is during its contraction, or during its dilatation by the blood entering from the veins and auricles, that the heart strikes against the ribs.

(1.) Till latterly, the heart's impulse had been generally attributed to the contraction of the ventricles. Some imagined that the ventricles during the systole become lengthened, and from that cause strike the walls of the chest by their apex. No such lengthening, however, takes place. Senac* attributed the impulse to the distension of the arteries by the blood during the contraction of the ventricles, to the filling of the auricles at the same time, and to the straightening of the arch of the aorta by the impulse of the blood forced into it. But, as Carson has remarked, it is an error to suppose that an arched and moveable tube has a tendency to become straight when fluid is injected into it, for the pressure of the fluid on its walls is equally strong in all directions.

(2.) Corrigan, Stokes, and Burdach have very recently advanced the doctrine that the impulse of the heart against the thoracic parietes is produced by the distension of the ventricles at the moment that it is brought to its greatest degree by the contraction of the auricles, and consequently that it precedes the contraction of the ventricles.† To inform myself, if possible, whether this view is correct, I made some experiments on a goat whose thorax was opened during life; Professor Albers was present. Our observations, however, did not convince us that the opinion of Corrigan, Stokes, and Burdach is the correct one; on the contrary, while the animal lay on its back, we saw distinctly that the heart was elevated at every contraction of the ventricles, and the apex particularly. When the hand was laid upon the heart, the shock during the contraction of the ventricles was so forcible and instantaneous that it seemed impossible to attribute the heart's beat or the impulse against the ribs to any other cause, while during the diastole we felt no shock. The heart does not, however, recede from the thoracic parietes during the

* Traité de la structure du Cœur. Paris, 1749.

† See Burdach's Physiol. vol. iv. p. 219—222.

diastole. During life, the heart lies with its apex close to the walls of the chest, and the shock communicated to these walls by the heart by the contraction of the ventricles is felt externally, constituting the heart's impulse; to give the shock, the heart does not require any great change of position.

Sounds of the heart.—When the ear, or a stethoscope, is placed over the precordial region, two sounds are heard following each other quickly at every beat of the heart. I have sometimes heard them in my own person at night when lying on the left side. Like the heart's impulse, these sounds are followed by a pause. The interval of time between the two sounds compared with the pause is, according to my observation, in the proportion of 1 to 3, or about $\frac{1}{4}$th of the time occupied by the beat and pause together,—that is, about $\frac{1}{5}$th of a second. From repeated and long continued observations I am satisfied that the first sound is synchronous with the impulse at the chest, and nearly synchronous also with the pulse of the facial artery, which is only $\frac{1}{30}$th of a second later than the impulse at the chest. The extent to which the first sound was distinctly heard in a healthy female did not exceed the space in which the impulse was felt; but the second sound was audible in nearly the whole extent of the chest, as high as the clavicles. In pregnant women the two sounds of the fœtal heart are heard through the abdominal parietes.

Laennec attributed the first sound to the contraction of the ventricles; the second he ascribed to the action of the auricles, which, however, is indubitably an error, since the contraction of the auricles immediately precedes the contraction of the ventricles. Corrigan, Stokes, Pigeaux, and Burdach attribute the first sound to the contraction of the auricles, the second to the contraction of the ventricles. Now the arterial pulse, which is known to depend on the contraction of the ventricles, is nearly synchronous with the heart's impulse, being only $\frac{1}{30}$th of a second later than it; while the second sound is not heard until $\frac{1}{5}$th of a second after the impulse. It is evident, therefore, that this second sound cannot be dependent on the contraction of the ventricles; and it is also evident that the impulse at the chest which is synchronous with the first sound cannot be ascribed to the distension of the ventricles and contraction of the auricles, as Burdach imagines.

Dr. Williams believes the first sound to be the effect of the contractions of the ventricles and auricles succeeding each other with great rapidity; the second sound he attributes to the action of the valves. Despine maintains, that the first sound is the effect of the contraction of the ventricles, the second that of their dilatation.* Dr. Hope considers the first sound to be the effect of the contraction of the ventricles, which the contraction of the auricles precedes; the second sound to be the effect of distension of the ventricles by the blood which is impelled by the *vis à*

* Burdach's Physiol. iv. bd. 223.

tergo from the veins into the auricle, and thence into the ventricle before the contraction of the auricle takes place.*

I forbear giving an opinion as to the exact mode of the production of the two sounds, and shall merely state a few facts which I think I have determined with considerable certainty. These facts are, that the interval between the two sounds is equal to $\frac{1}{4}$th the time occupied by an entire beat and pause; that the first sound is synchronous with the impulse; and that the arterial pulse is but a small fraction of a second later. Being convinced that the impulse is produced by the contraction of the ventricles, I am equally certain that the first sound also arises from the contraction, the second from the dilatation of the ventricles. Magendie† states, as the result of his more recent experiments, that the sounds cease as soon as the thorax of the animal is opened, and return again when a hard body is laid upon the heart to receive its impulses. He attributes the first sound, as we do, to the contraction of the ventricles, and to the impulse of the apex of the heart against the ribs; the second sound to a similar impulse produced by the dilatation.‡

We now pass to the description of the greater and lesser circulation. The greater circulation is the course of the blood from the left side of the heart through the arteries of the body, and back again through the veins to the right side of the heart. The course of the blood from the right side of the heart through the pulmonary arteries to the lungs, and back to the left side of the heart through the pulmonary veins, is called the lesser circulation. The blood therefore in fact makes but one circuit, of which there are two divisions; in each of these the blood passes through capillary vessels from arteries to veins.

a. Lesser or pulmonary circulation.

The same quantity of blood enters the right auricle from the superior and inferior cavæ, and from the great coronary veins, as is impelled during the same period of time by the left ventricle through the arteries of the body. On the contraction of the auricle, the entrance of the blood of the veins is suddenly interrupted; but, when the auricle becomes relaxed, the blood rushes into it, and into the right ventricle as soon as its contraction also ceases. The auricle now contracts, and immediately afterwards the ventricle. The auricle contracting forces the blood through that orifice which remains free. It cannot regurgitate into the venæ

* Froriep's Notiz. 735. See Dr. Hope's Treatise on Diseases of the Heart.

† Ann. des sc. nat. 1834.

‡ [The experiments of M. Magendie have been repeated by Dr. Hope and M. Bouilland, and the results were unfavourable to his theory. M. Bouilland attributes both sounds to the action of the valves. Dr. Carswell was the first who, led by the observation of some cases of disease of the heart and aorta, suspected that the second sound was produced by the closing of the sigmoid valves by the pressure of the columns of blood in the aorta and pulmonary artery.]

cavæ, because it is in them opposed by the stream of venous blood which continues to be impelled towards the heart by the *vis à tergo;* and the opening of the coronary veins is closed, its valve being applied to the orifice by the pressure of the blood in the auricle. The blood flows therefore into the right ventricle, which during the contraction of the auricle had become partially dilated and is now completely distended. While the right auricle is again dilating to receive the blood of the veins, the right ventricle contracts; and the blood, which cannot regurgitate into the auricle on account of the tricuspid valve being spread out by the pressure of the blood so as to close the auriculo-ventricular orifice, is driven into the pulmonary artery.

In this manner the venous blood returning from the body is, by the agency of the right side of the heart, transmitted to the pulmonary circulation. All the blood contained in the auricle is not, however, forced by its contraction into the ventricle. A portion regurgitates into the superior and inferior vena cava; or, at any rate, the contraction of the auricle checks the flow of blood from the venous trunks towards the heart, which otherwise must continue uninterruptedly. When animals are opened during life, the great veins are seen to become turgid at the time of each contraction of the auricle; and in the larva of the triton I have seen the blood, in the inferior cava and hepatic veins, advance in periodic jerks only. When the escape of the blood from the ventricle into the pulmonary artery is impeded from any cause,—whether from organic change in the pulmonary artery, ossification of the semilunar valves, or impediment to the motion of the blood in the lungs,—the regurgitation into the veins is necessarily increased. The regurgitation, or rather, periodic arrest of the blood in the great venous trunks, is called the pulsus venosus. It cannot extend far, on account of the yielding nature of the vein; that portion only of the venous system which is near the heart is affected by it.

The blood, once in the arteria pulmonalis, cannot return when the ventricle becomes relaxed, because the column of blood in the artery itself spreads out the semilunar valves at the mouth of the artery and closes it. The course of the blood from the right ventricle, through the lungs, to the left side of the heart, is called the lesser circulation; it does not really form a circle, for the blood does not return to the point from which it started. It is only a part of the course of the whole circulation, and would be better named the pulmonic course of the blood, in opposition to the systemic course of the blood, which together with it forms an entire circuit or circulation. In the pulmonic course, the venous blood expelled from the right ventricle by successive new portions of blood, flows from the branches of the pulmonary artery into the capillary vessels of the lungs, and through these capillary vessels,—in its transit through which it becomes scarlet, or arterial,—into the pulmonary veins, and is by these poured into the left auricle. The capillary vessels in the lungs are, as in

other parts, the net-work of minute vessels, which intervene between the smallest branches of the arteries and the radicles of the veins; but here the meshes of the net-work are extraordinarily small. The innumerable capillaries, that constitute the net-work, are enclosed in the delicate membrane forming the cells in which the last branches of the bronchi terminate. The mėmbrane that forms the cells is a continuation of the mucous membrane of the trachea, and is, consequently, continuous throughout the lungs. The lungs, therefore, — omitting from consideration the bronchial tubes, arteries and veins,—must be regarded as a delicate membrane traversed by a net-work of capillary vessels and folded in the form of cells, so as to produce a very extensive surface in a small space; the process of respiration being effected by the contact of the air, which enters by the bronchi, with the inner surface of these cells, in the parietes of which the particles of blood circulate in most minute currents.

In the simpler animals, as in the naked amphibia, the lungs are, indeed, mere sacs, with internal cellular folds. In branchiæ also,—the second form of respiratory organ,—the essential character is the great developement of surface in a small space; but in them the developement of respiratory surface is towards the exterior; in the lungs it is towards the interior, either in the form of sacs or of ramified tubes. In branchiæ, as in lungs, the blood is distributed over an immense extent of surface, by means of the reticulated capillary vessels of all the branchial plates and lamellæ, each of which has its small artery, which, at the extremity of the lamella, is reflected into a small vein, while numerous capillary branches keep up anastomoses between the two, across the breadth of the branchial lamella. In frogs and salamanders, the motion of the blood through the capillary vessels of the sacculated lungs can be subjected to observation by means of the microscope.* The spaces between the streams of blood are, according to my observations, islets, distributed with perfect regularity, and scarcely larger in diameter than the currents themselves. The motion of the blood is seen still more distinctly in the capillary vessels of the branchiæ of the larva of the salamander.† The branches of the pulmonary arteries and veins in the lungs of salamanders, frogs, and toads, according to Dr. Marshall Hall's description,‡ which is most exact, run constantly parallel to each other; in the angle formed by two arterial branches, there is always a venous branch, in the angles between two venous branches always a branch of an artery. In the

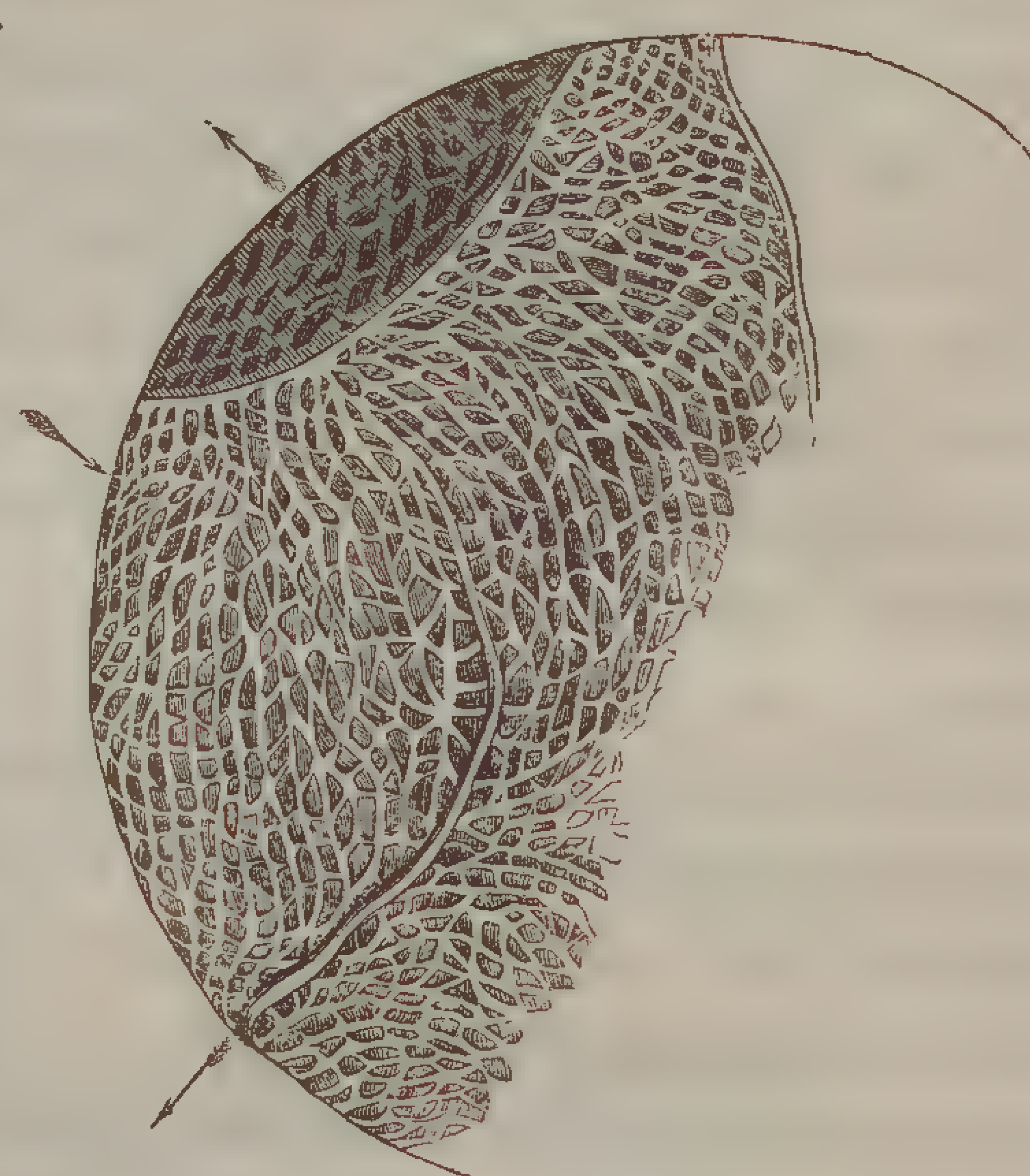
* See the representations of Cowper, in Philos. Transact. abridged, vol. v. p. 331; of the lungs of the salamander, by Prevost and Dumas, in Magendie's Physiology, t. ii. and in Dr. Milligan's translation.

† Rusconi, Della circolazione delle larve delle Salam. aquat. Pavia, 1817. Amours des Salam. aquat., Milan, 1821, in which, however, the transverse branches of the branchial laminæ are not noticed. Steinbach, Analecten für Naturkunde. Fürth, 1802.

‡ A Critical and Experimental Essay on the Circulation of the Blood; London, 1831; plates 5—8.

septa of the pulmonary cells, which project into the interior of the lungs, the arterial and venous branches are so distributed that the small venous twigs run along the inner border of the septa. The ultimate branches of the arteries and veins terminate abruptly in an intermediate net-work of capillaries (fig. 13); while, in all other organs, the ramification of the vessels still continues, passing imperceptibly into the capillary net-work. The ultimate branches of the pulmonary arteries and veins are throughout perforated like sieves, to give off and receive the blood of the capillary vessels. Dr. Marshall Hall's representations of the capillary circulation in different parts are extremely interesting, particularly the 8th plate.

Fig. 13.*



Destruction of the capillary net-work of the pulmonary cells and of the air-cells themselves by inflammation, suppuration, or structural degenerations, has two very important consequences; in the first place, diminution of the respiring surface, the effect of which may be imperfect formation of the blood, and at last wasting of the body; secondly, diminution of the number of channels through which the blood must pass, and, consequently, impediment to its course from the right to the left cavities of the heart, and thence to the general system. In warm-blooded animals, in which all the blood must pass through the capillary system of the lungs before it can arrive at the great aortic circulation, any diminution of the extent of this pulmonic capillary system must be productive of impediment to the circulation generally; and, in patients suffering under pulmonary disease, excessive action of the heart, tendency to congestion of blood in the lungs, disposition to inflammation of these organs, and feverish excitement, must be frequently observed. Any other organ might be wholly destroyed without the circulation being impeded in the other organs of the body, but the loss of a portion of the lungs is a source of obstruction to the circulation generally; hence it is evident that persons suffering with pulmonary disease ought to avoid every thing which might produce still greater impediment and excitement in the circulation. From this consideration may also be explained why extensive destruction of other parts, unless accompanied by a constant draining of the fluids of the body, do not always excite fever,

* [Fig. 13, representing the circulation in the lung of the toad, is copied from the plate in Dr. Marshall Hall's work, to which our author alludes. The arrows indicate the course of the blood.]

while diseases affecting the substance of the lungs are so prone to be attended with hectic. Disorganisation in other parts ordinarily produces merely the local effects of impediments to the circulation; for instance, congestion of blood and effusion of serum, in the form of local dropsies, —such as ascites, in cases of disorganisation of the liver, &c.—a termination in effusion, which is proportionally rare in cases of disorganisation of the lungs. Gaspard has shown, that death is inevitable, and comes on very rapidly, when the circulation in the capillary vessels of the lungs is obstructed by foreign substances; for instance, by oil, mucus, metallic mercury, powdered charcoal, and powdered sulphur, injected into the veins.

The pulmonary circulation would be perfectly isolated from that of the body, were it not that the bronchial arteries communicate with the small branches of the pulmonary artery. When the pulmonary artery and its branches are narrowed, the anastomoses between them and the bronchial arteries become enlarged.

If the chemical changes which the blood undergoes in the lungs are arrested by suspension of the respiratory movements, or by breathing irrespirable gases, the blood ceases to acquire the arterial character in the lungs, and returns of a dark red colour.

b. Greater or systemic circulation.

The blood, having assumed its arterial colour, flows from the pulmonary veins into the left auricle; and then commences the greater circulation, or, more correctly, the systemic portion of the circulation, in which the blood is impelled into the arteries, and from thence into the capillary system of the body, where it acquires a dark red colour, and returns from the capillaries through the veins to the right side of the heart. When the auricles dilate, the blood of the pulmonary veins rushes into the left auricle, and a part of it enters the left ventricle. As soon as the muscular contraction of the ventricle has ceased, the auricle contracts, and impels the blood into the dilated ventricle, which is thus filled to its greatest capacity. During the contraction of the left ventricle which now follows, the mitral valve closes the auriculo-ventricular orifice; and the blood, forcing asunder the semilunar valves at the mouth of the aorta, flows into that vessel. Reflux from the aorta into the ventricle cannot occur, for the blood, re-acted upon by the elastic coats of the vessel, presses down the pouch-shaped semilunar valves so as to close the aortic orifice. The left ventricle contracts with much greater force than the right ventricle, the walls of the former being in the adult, as is well known, three times thicker than those of the latter. The left ventricle requires greater power on account of the systemic circulation being more extensive than the pulmonic circulation, and on account of the much greater resistance which must be produced by friction in the capillary vessels of all the organs of the body.

From the aorta the blood forced onwards at each beat of the heart by a new mass ejected from the ventricle, is distributed throughout the whole body with the exception of the lungs, and passes through the capillary vessels into the veins.

During violent bodily exertion, the motion of the blood in the capillary vessels must be interrupted in a great part of the body in consequence of the compression of vessels by the numerous muscles which are repeatedly contracting. The more extended the operation of this cause of obstruction is, the more it resembles that interruption of the circulation which is produced by even slight obstructions in the lungs. Similar effects also are produced; the column of blood offers a greater resistance than usual to the power of the heart; the blood does not circulate freely and quickly enough through the lungs, and becomes accumulated there, so that deficient aeration of the blood is at the same time induced. Hence the labour of respiration during such great exertions, which is attributed, but less correctly, to an increased call for arterial blood on such occasions. The continued contraction of the muscles in cases where single limbs are kept for a long time in action, is also accompanied with accumulation of blood in these parts. In some animals which keep their limbs for a long time in continued action in climbing, nature has avoided the interruption of the circulation,—at least that produced by compression of the arteries,—by the immediate division of the arterial trunks of the extremities wholly or in part into a vast number of small anastomosing branches. Such a provision is seen in the bradypus, myrmecophaga, manis, and stenops; it occurs both in the vessels of the limbs, and in those of the tail, which is also used in climbing.*

The smaller arteries in every organ of the body before they become capillary are connected by repeated anastomoses with each other, as may be seen in any finely injected membrane; and many parts of the body receive blood by large arteries which arise from very different parts of the vascular system; thus the brain is supplied from the internal carotid and vertebral artery, and the communication between the epigastric, mammary, and intercostal arteries is well known; similar anastomoses

* Sir A. Carlisle, Philosoph. Trans. 1800. Vrolik, De peculiari art. extrem. in nonnullis animalibus dispositione. Amsterd. 1826. Meckel, Vergleich. Anat. v. 339. Several other arterial plexuses are still enigmatical: for instance, the rete mirabile found in several mammalia, and which in the ruminantia and hog is formed from cerebral branches of the common carotid; all its branches again uniting to form the cerebral carotid. Rapp (Meckel's Archiv. 1827) shows that in animals with a rete mirabile the vertebral artery does not go to the brain, and is either connected with the external carotid artery, as in the goat and calf, or, at the same time that it is connected with the rete mirabile, is also distributed to the cervical muscles, as is the case in the sheep. Similar net-works of arteries occur in the orbit of ruminantia, cats, and birds, according to Rapp and Backow (Meckel's Archiv. 1829); and in these cases the arteries of the globe arise from the arterial plexus. In some birds a rete mirabile is situated on the arteria tibialis antica.

are met with in all parts of the body. The capillary system of all connected parts being continuous, all the vessels of the body, whether arteries or veins, are also connected through the medium of it. The capillary vessels of the whole body and the anastomoses of the arteries form in this manner an uninterrupted net-work, which receives blood from innumerable arteries, and can be supplied with blood directly or indirectly from different sources. If the vessel which usually conveys blood to a part is obstructed, new ways of supply are developed by the simple dilatation of already existing communications without new vessels being formed. Thus is explained the phenomenon of collateral circulation, or the restoration of the circulation through a part after obliteration of its principal vessel. At first a number of anastomosing branches are dilated, and by degrees distinct vessels, of considerable size, are again developed from among them. In animals, the aorta abdominalis even may be tied without an absolutely fatal result. This operation has been performed twice on man, but in each case death ensued. But all the other great arteries which are accessible in the human subject have been tied in cases where it was necessary, with success. There are, indeed, cases recorded, proving, that when it takes place slowly, even the obliteration of the aorta immediately below the origin of the arteries of the upper part of the body does not preclude the developement of a collateral circulation, the blood again finding its way circuitously to the part of the aorta below the obliteration by dilatation of anastomoses between the internal mammary, first intercostal artery, and the intercostal branches from the aorta.* In a case of this kind, described by Reynaud,† the principal communications between the subclavian artery of each side and the part of the aorta below the obliteration were effected by anastomoses of the arteria cervicalis profunda, transversalis cervicis, and intercostalis prima with the intercostal arteries of the thoracic aorta, and between the subclavian and crural arteries by direct inosculation of the internal mammary and epigastric.

The blood distributed through the arteries being impelled onwards by the new masses constantly ejected from the left ventricle, follows the course indicated through the vessels, and from the minute arteries is transmitted through the capillaries into the minute veins. This transit from arteries to veins can be observed by means of the microscope in many transparent parts; so that its existence is not merely deduced from the course which the blood is known to take in the arteries and veins, but is an object of direct observation.

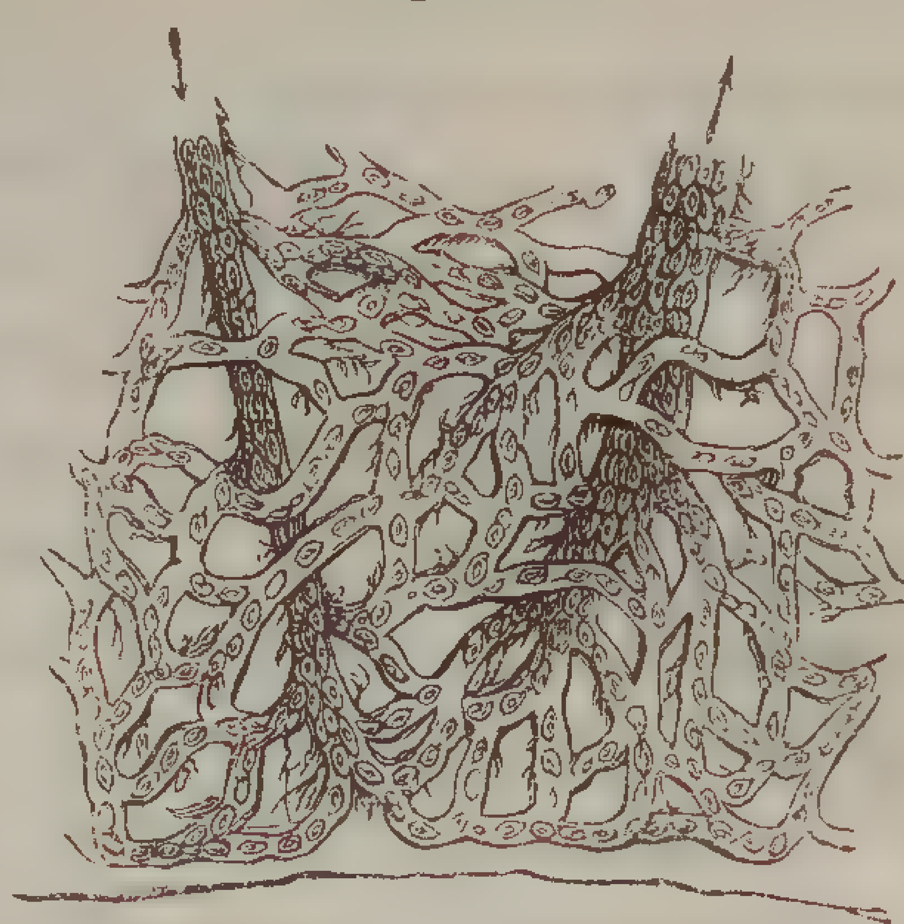
The web of the frog's foot (fig. 14), the tail of young fishes, of the larvæ of the salamander, frog, or toad, the mesentery of all mammalia, the wings

* See the case observed by A. Meckel. Meckel's Archiv. 1827.

† Froriep's Notiz. 537.

of the bat, the germinal membrane of the egg of oviparous animals, are all well adapted for seeing the capillary circulation.*

Fig. 14.†



The red corpuscules are distinctly seen flowing from the minute ramifying arteries into a net-work of vessels of nearly equal size throughout, and again collecting from this net-work into the radicles of the veins, which, by their successive reunion, form larger trunks. (See fig. 14.)

In the finest capillary vessels the red particles flow one after another in a single series, which is frequently interrupted for a time: when they flow thus singly, they appear almost colourless; when accumulated together in greater number, they appear yellow; and when in still larger quantity, they are yellowish red or red.‡

The blood during its passage through the capillary vessels becomes of a dark red colour. The motion of the blood in the veins is continuous, not pulsatory as in the arteries. Those veins which are exposed to the pressure of muscles, have pouch-like valves which prevent the backward passage of the blood towards the capillaries, consequently, any pressure on the veins, instead of interrupting, favours the flow of the blood towards the heart. In the veins of parts protected from external pressure the valves do not exist. In the pulmonary veins Mayer has discovered incomplete valves. E. H. Weber has observed valves in the portal vein of the horse; they do not exist in man.

c. Portal circulation.

The blood of the spleen, intestinal canal, stomach, pancreas, and mesentery is not returned immediately to the vena cava; the veins

* See the representation of the capillary vessels carrying blood, of the area vasculosa of the egg in Pander's Entwickelungs-geschichte des Hühnchens im Ei; of young fishes in Doellinger's Denkschrift der Akad. der Wissenschaft. zu München, Bd. vii.; of the web of the frog's foot in Schultze's Lebens-process im Blute, Berlin, 1822, and in Marshall Hall on circulation, tab. iii.; of different parts of frogs and mammalia, Kaltenbrunner, Exp. circa statum sanguin. et vas. in inflammatione, Monach, 1826; of the mesentery of the frog, Reichel, De sanguine ejusque motu, Lips. 1767, Marshall Hall, l. c. t. iv.; of the tail of the stickleback, M. Hall, l. c. t. i.; of the embryos and larvæ of fishes, frogs, and salamanders, Baumgaertner über Nerven und Blut, Freiburg, 1830.

† Capillaries in the web of the frog's foot magnified.—This is reduced from the representation given by Dr. A. Thomson in the Cyclopædia of Anatomy. The engraver has not preserved accurately the proportion between the size of the capillaries and the space in which they run; the capillaries are somewhat too large. But the diagram shows the relation of the minute arteries and veins to the capillary net-work in the systemic circulation as compared with the pulmonic circulation. (See fig. 13.)

‡ On the circulation in the capillaries, see page 218.

of these organs unite to form the vena portæ, by which their blood is in the first place poured into the capillary system of the liver, (which also receives blood from the hepatic artery,) and is thence conveyed by hepatic veins to the cava.* Professor Retzius of Stockholm, however, has informed me that he has discovered in man some minute communications between the veins of the intestines and the branches of the vena cava. When he injected the vena cava and vena portæ with fine injection of different colours, he found that the whole mesocolon and colon sinistrum were injected with both colours, and veins belonging to the two systems at several places formed anastomoses. The veins of the colon and mesocolon, which belonged to the system of the vena cava and entered the left renal vein, lay superficially, while those which belonged to the vena portæ lay for the most part nearer the mucous membrane. The external surface of the duodenum also had received injection from the vena cava. M. Breschet too has filled the inferior mesenteric vein from branches of the inferior cava, and Schlemm has discovered distinct communications of the inferior mesenteric vein with branches of the inferior cava about the anus. From this fact the suggestion may be drawn that in obstructions and congestions of blood, perhaps even in inflammations of the intestinal canal, abstractions of blood from about the anus will be of service.

The blood of the portal vein of all the vertebrata,—and the blood of the afferent renal veins in fishes, amphibia, and reptiles,—has a second time to overcome the resistance offered by the minute canals of a capillary system, before it reaches the heart. I have discovered that in the larvæ of the salamander, the circulation in the liver can be distinctly seen when viewed as an opaque object with a simple microscope.† The blood of the porta in its passage through the capillary vessels of the liver into the hepatic veins is seen to run in the interstices only of the acini, and the single particles of the blood can be as clearly distinguished as in transparent parts.

The blood in the vena cava, as well as in all the venous canals of the liver, flows in jets, probably from the advance of the blood being checked by each contraction of the right auricle, or of the inferior vena cava itself, which in frogs can be seen to contract periodically. There is no observable difference in the colour of the blood in the vena cava, the vena portæ, and the hepatic veins.

Rate of the blood's motion.—After this general description of the circulation of the blood, it remains for us to discuss the rate of its motion and the time in which it completes its entire circuit. The rate of the blood's motion in the vessels must not be judged of by the rapidity with which it flows from a vessel when divided. In the latter case,

* See page 169.

† Meckel's Archiv. 1828. See the drawing in my treatise, De gland. penit. struct. tab. x. fig. 10.

the rate of motion is the result of the entire pressure to which the whole mass of blood is subjected in the vascular system, and which at the point of the incision in the vessel meets with no resistance. In the closed vessels, on the contrary, no portion of blood can be moved forwards but by impelling on the whole mass, and by overcoming the resistance arising from friction in the smaller vessels. With respect to the time in which the circulation of a single portion of blood is completed, the following results have been deduced by Hering from eighteen experiments on horses. The time required for the passage of a solution of ferrocyanate of potash of different strengths, which is mixed with the blood, from one jugular vein (through the right side of the heart, the pulmonary circulation, the left cavities of the heart, and the general circulation) to the jugular vein of the opposite side, varies from twenty to twenty-five or thirty seconds; from the jugular vein to the great saphena it is only twenty seconds, from the jugular vein to the masseteric artery between fifteen and thirty seconds, to the facial artery in one experiment between ten and fifteen seconds, in another experiment between twenty and twenty-five seconds; in its passage from the jugular vein to the metatarsal artery it occupied between twenty and thirty seconds, and in one instance more than forty seconds. The result was nearly the same whatever was the rate of the heart's action. These results do not, however, accord with the estimate of the time occupied by the circulation, which is deduced from the quantities of blood generally supposed to be contained in the body, and from the quantity which can be advanced at each beat of the heart. According to Wrisberg, a woman lost by a fatal flooding twenty-six pounds of blood, and in the beheading of a full-blooded woman twenty-four pounds of blood were collected. If we suppose two ounces of blood to be impelled forward at every beat of the heart, it would require one hundred and sixty beats for the circulation of twenty pounds; and for the circulation of ten pounds of blood, which Herbst* calculates to be the quantity of blood contained in the human body, eighty beats of the heart would be required. It may, therefore, be admitted with more certainty that the circulation of the blood in man is completed in from eighty to two hundred and fourteen beats of the heart, or in from one to two minutes.†

The time in which the blood performs its course from one side of the heart to the other, varies much according to the organ it has to traverse. The blood which circulates from the left ventricle, through the coronary vessels to the right side of the heart, requires a very far shorter time for the completion of its course than the blood which flows from the left side of the heart to the feet, and back again to the right side of the heart; so that the circulation from the left to the right

* De sanguin. quantit. Göttingen, 1822.

† See Burdach's Physiologie, iv. p. 101 to 253.

cavities of the heart forms a number of arches, varying in size *ad infinitum*, the smallest of these arches being formed by the circulation through the coronary or nutritious vessels of the heart itself. The course of the blood from the right side of the heart, through the lungs, to the left, is shorter than most of the arches described by the systemic circulation, and in it the blood flows, *cæteris paribus*, much quicker than in most of the vessels which belong to the aortic circulation. Although the quantity of blood contained in the greater circulation of the body, on account of its greater extent, is very far greater than the quantity within the lesser circulation, yet at any imaginary spot of the pulmonary artery, in a certain space of time, just as much blood passes as at any imagined point in the aorta; for, although in the capillaries the circulation is subject to great variation, in the main trunks of the closed circuit no more blood can leave one point than finds place at another point. If, therefore, we suppose the capillary vessels between arteries and veins to be equally large in the lungs and the rest of the body, a far greater number of them must be included in the same space in the lungs than in other parts of the body. This is found by observation to be the case, for in the lungs of frogs the interspaces between the capillaries are scarcely larger, in man even smaller perhaps, than the diameter of the capillary vessels themselves.* This has been shown by Cowper, Wedemeyer, Marshall Hall, Prevost and Dumas, Weber (in the human subject), and more recently by myself.

Lastly, it is to be remarked, that the rapidity of the motion of the blood in the small branches must necessarily be less than in the trunks generally, if, as seems to be the case, the aggregate area of the branches of a stem is larger than the area of the stem itself, although this must not be regarded as strictly proved. If, however, we imagine all the small vessels of any single organ united into one trunk, and the blood to flow in a circular course from the artery into this trunk, and thence through the vein into the artery again, thus forming a closed circle, although the movement of the single particles of the blood will be more rapid in those parts of the circle where the tube is narrow, and slower where the tube is wider, still within a given time the same volume of blood must pass each and every point of the circle.

CHAPTER III.

OF THE HEART CONSIDERED AS THE CAUSE OF THE CIRCULATION OF THE BLOOD.

The heart, like other muscular organs, contracts when irritated mechanically, or by galvanism. Sœmmering, Behrends, and Bichât denied the influence of galvanism on the heart, but I have frequently repeated Humboldt's and Fowler's experiments, and have obtained the same results as they did. In both frogs and dogs, in which the heart had ceased to act, I have re-excited its contractions by means of a single pair of

* See page 179.

plates, or a weak galvanic pile. But the heart, with most other organs which are endued with involuntary motion only, such as the intestinal canal, is distinguished from voluntary muscles, by the irritation exciting in it not a single contraction, but a succession of periodic contractions.

The heart being thus, like all muscles, excited to action by a stimulus, it is very natural to conclude that the blood contained in its cavities supplies the stimulus during life; and this supposition is strengthened by the circumstance of the heart's action becoming more feeble in proportion as the quantity of blood it contains is diminished.

To explain why the contractions are rhythmic, it has been said that the same act—the systole—by which the heart expels its stimulus—the blood—in one direction, causes its cavities to be again filled with blood from the veins. In the same way the alternation of the contractions of the auricles and ventricles may be explained, since the one cavity by its contraction gives rise to the filling of the other. But however necessary a certain quantity of blood and a certain distension of the cavities of the heart may be for the preservation of its action, and however certain the effect of every mechanical dilatation of the heart from within may be in exciting its contraction, yet the stimulus of the blood in its cavities cannot be the primary cause of the contractions of the heart, for the heart still continues to contract, though feebly, when emptied of its blood. The regular succession of the heart's contractions may be explained in another way. The heart, at each systole, expels the blood from its nutritive vessels, which, when the contraction ceases, are again re-filled by the agency of the elastic coats of the arteries, which exert a constant pressure on the blood contained in them. The re-filling of the minute vessels of the heart with blood during each diastole may be supposed to become the cause of a fresh contraction. This hypothesis, however, is refuted by the same fact as the former; for the heart, particularly that of amphibia and fishes, continues to contract regularly—the auricle and ventricle in the same succession—when it is removed from the body and emptied of its blood; in amphibia, indeed, the action continues for hours. This might, however, be explained by attributing it to the stimulus of the atmosphere, which, although its action is constant, may nevertheless excite periodic contractions.* But the action continues in a vacuum, and an external cause like the air does not explain the regular succession of the ventricular contractions after those of the auricles. The cause, then, must be in some way connected with the organisation of the heart, and with the constant mutual action which is going on between the blood in the capillaries, or the cardiac nerves, with the texture of the heart; and whether the cause be constant in its action or periodic, the rhythmic contractions of the heart are equally explicable. The nature of the cause, however, cannot be determined in the present state of our knowledge.

* In accordance with the law of excitability stated at page 57.

1. *Influence of the respiration on the heart's action.*—When the chemical changes effected in the blood in the lungs are interrupted,—whether it be from the respiratory movements being checked, in consequence of lesion of the nerves on which they depend,—whether it be from mechanical impediments to the movements, or from the inhalation of irrespirable gases,—the vital action of all the organs of the body is depressed, and, in the higher animals, is indeed soon annihilated. It is true, the blood no longer arterialised, continues for a time, as Bichât and Emmert have shown,* to move in the arteries; and the heart, after the apparent death of the body, generally continues to beat slowly and feebly even in warm-blooded animals during more than half an hour; nevertheless, interruption of respiration enfeebles its action to such a degree, that the circulation very soon ceases; while, on the other hand, if, (after the respiratory movements have been interrupted by injuries of the encephalon, but particularly of the medulla oblongata, or by poisoning,) artificial respiration be performed, the circulation may be maintained for a much longer period, whatever be the animal on which the experiment is instituted. In a dog beheaded after tying the cervical vessels, and in which artificial respiration was kept up, Brodie saw the heart continue to beat for two hours and a half, in which space of time there were thirty-five pulsations; and, in another dog, an hour and a half, during which period there were thirty pulsations:† so that the influence of the respiration on the heart's action seems to be greater than that of the nervous system. In cold-blooded animals, however, this influence of the respiration, or of arterialised blood, on the heart is much less evident; for frogs, the lungs of which I had tied and removed, have lived thirty hours afterwards, the action of the heart still continuing; while, after destruction of the brain and spinal marrow in these animals, the action of the heart ceases much sooner, namely, in six hours: consequently, either the function of respiration in frogs can, after removal of the lungs, be supplied by the skin, or the brain and spinal marrow are in these animals much more necessary to the maintenance of the heart's action than respiration. The latter is most probably the more correct explanation, for when they can breathe neither by the lungs nor by the skin, namely, when they are immersed in pure hydrogen, frogs live more than twelve hours, as I have myself witnessed. The final suspension of the heart's action, in cases where respiration is suspended, may indeed depend chiefly on the change which ensues in the nervous system when it no longer receives red blood.

The disturbance of the circulation, after interruption of the respiration in the higher animals, is certainly not produced by the collapse of the lungs; for, although these organs in the collapsed state might offer some impediment to the passage of the blood, the motion of the blood

* Reil's Archiv. v. p. 401.

† Reil's Archiv. xii. p. 140.

in the arteries, as Bichât and Emmert showed, continues in such cases for a certain time undisturbed.

Dr. Goodwin attributed the depression of the circulatory powers, after interruption of the respiration in the higher animals, to the circumstance of the left ventricle ceasing to receive arterial blood, and supposed that the influence of this kind of blood was indispensably necessary to the action of the left side of the heart. To this Bichât replied, that in animals of which the respiration is suspended, the dark blood coming from the lungs to the heart does not cause the *immediate* cessation of the contractions. This and other arguments adduced by Bichât* are not conclusive. It is not, however, at all probable that each side of the heart has a specific irritability for different kinds of blood; for in the fœtus, in which the auricles communicate by the foramen ovale, and in which there is no pulmonary respiration, but only some peculiar change effected in the blood in its passage through the placenta, both sides of the heart receive the same kind of blood. If the immediate action of bright red blood on the heart is really necessary to the maintenance of its action, Bichât's explanation is much the more probable. He supposes that interruption of the respiration deprives the heart of its irritability, by preventing the supply of arterialised blood to the muscular fibres by the coronary arteries, which now carry dark venous blood. But although it appears certain that arterial blood does exert an influence on the heart's action, yet the relative degree in which this influence and that of the nerves are necessary cannot be estimated, for all disturbances of the respiration produce corresponding disturbance in the action of the nervous system.

2. *Influence of the nerves on the heart's action.*—The influence of the passions, and other affections of the nervous system, on the heart's action, is matter of constant observation. All sudden passions at first disturb and then accelerate its action; the contractions being much more vigorous and frequent under the influence of the exciting passions, while they are rendered feeble, at the same time that they are accelerated by the depressing passions.

Nevertheless, some persons have denied the dependence of the heart on nervous influence. Thus Haller denied it, because the heart continues to contract when removed from the body, and because irritation of the cardiac nerves does not produce those convulsive actions which irritation of the nerves of other muscles gives rise to.

The first researches on this subject are those of Sœmmering and Behrends on the cardiac nerves, in 1792, which tended to prove that the substance of the heart receives no nerves, and that all the fibres of the cardiac nerves in the heart are distributed to the coats of the cardiac vessels. This seemed to confirm Haller's doctrine of the contractility of the muscles, namely, that this power is inherent in the muscles them-

* Rech. sur la vie et la mort.

selves, and not dependent on the influence of the nerves, and that the nerves excite contractions in the muscles in the same way as external stimuli, whether mechanical, electrical, or chemical; and it would follow, that the heart not being endowed with the nervous stimulus, is stimulated to motion by the blood itself. The experiments of Sœmmering and Behrends, to show that galvanism produces no contraction of the heart, while it has this effect in all muscles provided with nerves, seemed to confirm this view still more strongly.

But Scarpa has demonstrated that the cardiac nerves are really distributed in great abundance to the muscular substance of the heart. Humboldt, Pfaff, Fowler, and Wedemeyer have succeeded in producing contractions of the heart by means of galvanism; and I have repeated their experiments with success in frogs as well as in mammalia. Humboldt* states that by galvanising the cardiac nerves he has produced contractions of the heart. The nerves may, as Burdach rightly remarks, act as moist conductors when one wire of the battery is applied to them, the other to the heart; Burdach,† however, actually saw the contractions of the heart of a dead rabbit become stronger when he applied both wires of the pile to the cervical portion of the sympathetic nerves, or to the inferior cervical ganglion. Such experiments on the motor power of the nerves are not conclusive unless the wires are applied to the nerves alone, and unless the galvanic action is very weak. Strong discharges may be transmitted through nerves acting as moist conductors merely, even to the heart itself. For this reason the experiments of Burdach, in which he re-accelerated the action of the heart of a dead rabbit, after it had begun to fail, by touching the sympathetic nerves with caustic potash or ammonia, are the more interesting; and particularly so, since, in a dead rabbit, painful impressions can no longer have any effect in changing the action of the heart. I did not, however, myself succeed in obtaining the same result in repeating this experiment. The experiments which Brachet ‡ and others have instituted on living animals, for the purpose of determining the irritability of the nerves, are of no value with regard to the heart, the heart's action being so much affected by painful impressions.

Another phenomenon which distinguishes the heart from other muscles is the persistence of its rhythmic contractions in their regular order in the different cavities, even when removed from the body and emptied of its blood. This cannot be explained otherwise than by supposing the heart under these circumstances to retain with its nerves some specific nervous influence. The influence of the nerves, therefore, seems to be the cause of its contractions; and this seems to be confirmed by the great effect which irritations of the brain and spinal

* Ueber die gereizte Muskel- und Nervenfaser, i. 342. † Physiol. iv. 464.
‡ Recherches sur le système ganglionaire.

marrow, and passions of the mind, have in modifying the action of the heart. If it were possible to destroy the vital function of the nerves, without at the same time depriving the muscles of their power of contraction, this question might be set at rest; but unfortunately the narcotic agents, which, when applied to the nerves, take from them their property of exciting—when irritated—contractions in the muscles to which they are distributed, render the muscles incapable of exercising their contractile power when the nerves are irritated. Opium applied to the heart of a frog soon puts a stop to its motion; when I employed the watery solution of opium which Humboldt used, I did not succeed. Although the dependence of the heart's action on nervous influence cannot be demonstrated in this manner, it is nevertheless evident that the nerves have a great share in its action, from the sudden disturbance and cessation of the rhythmic movements when the whole spinal marrow is suddenly destroyed.

Influence of the brain and spinal cord on the heart's action.—The inquiry respecting the part of the nervous system from whence this influence on the heart is derived, whether immediately from the cardiac nerves and sympathetic system, or through the medium of these from the spinal marrow and brain, was originated by Bichât. Before entering into this inquiry, it will be necessary to give a sketch of the principal divisions of the nervous system. The functions of the two systems of nerves were more exactly defined by Bichât. The nerves arising from the brain and spinal marrow have for the most part the power of exciting voluntary motion in the muscles to which they are distributed, but lose this power when their connection with the nervous centres is cut off; and the nerves arising from the spinal marrow are also deprived of the power of communicating volition when their connection with the brain is interrupted by injury of the spinal marrow. Nevertheless one of these nerves thus cut off from its source of volition—the nervous centres,—still retains for a time the power of exciting involuntary contractions of muscles when it is irritated mechanically or by galvanism.

The parts to which the branches of the sympathetic nerve are distributed, for example, the heart, intestines, and uterus, are endowed by them with involuntary motion only. The sympathetic nerve is connected with the brain and spinal marrow indirectly only, through the medium of the cerebro-spinal nerves. Bichât called the cerebro-spinal nerves "the nerves of animal life," the sympathetic nerves he styled the "nerves of organic life," and ascribed to the latter a certain independence of the brain and spinal marrow, regarding the ganglia and plexuses as their nervous centres. Recently a discovery has been made, which in the history of physiology ranks second only to the discovery of the circulation of the blood; it is, that the nerves which arise by an anterior

and posterior root from the spinal cord derive their power of exciting contractions in the muscles from the anterior root, and their power of sensation from the posterior root. This discovery is due to Bell. I have since proved that mechanical and galvanic stimuli applied to the posterior root have no power of exciting contraction in the muscles to which the spinal nerves are distributed.* Scarpa† not long since endeavoured to show that the connection of the sympathetic nerve in the chest with the commencement of the spinal nerves impl cates the posterior roots only of the latter nerves, and not their anterior roots; and consequently that the sympathetic nerve can neither be intended to communicate motor power to the heart from the spinal marrow, nor possess motor power itself. The researches of Wutzer and myself, as well as those of Retzius and Meyer, have shown, however, that Scarpa is incorrect, and that the rami communicantes inter nervum sympatheticum et nervos spinales receive their fibres from the anterior motor, as well as from the posterior sensitive roots of the spinal nerves.‡ The principal experiments made with a view to elucidate the influence of the spinal cord and brain on the motions of the heart are those of Legallois, Philip, Treviranus, Nasse, Wedemeyer, Clift, and Flourens.

The new facts brought forward by Legallois§ to prove that the cause of the heart's action resides in the spinal cord alone, may be reduced to the following heads: When the cervical portion of the spinal cord and medulla oblongata of an animal is destroyed, respiration ceases on account of the destruction of that part of the nervous centres from which the respiratory nerves arise; the action of the heart still continues, though too feebly to maintain the circulation, and the strength of the heart's contractions necessary for this purpose cannot be re-excited by artificial respiration. If the spinal cord is destroyed in successive portions at distinct intervals, the heart's action is supported longer than if it were suddenly destroyed. The circulation of the blood is also interrupted by the destruction of the inferior part of the spinal cord by thrusting a wire up the canal. In this case also it is not restored by artificial respiration. From these experiments Legallois concluded that the nervous power of the heart was derived from the spinal cord, and not from any particular portion of it, but from the whole cord. Legallois then reasoned that if this was true, after destruction of a part of the spinal marrow, the nervous influence of the uninjured part would no longer be sufficient to enable the heart to put in motion the whole mass of the blood, but that it would

* See Book iii.

† Scarpa, De gangliis nervorum, deque origine et essentia nerv. intercostalis; ad H. Weber. Annal. univers. d. medicina. Magg. e. Giugn, 1831.

‡ See Meckel's Archiv. 1831, i. p. 85 u. 260.

§ Exp. sur le principe de la vie. Paris, 1812.

certainly be sufficient, if artificial breathing was kept up, to force the blood through a part of the vascular system. Thus Legallois came to the conclusion that if, after partial destruction of the spinal marrow, the course of the blood through the vascular system was limited by tying certain vessels, the circulation would still be maintained in the course thus circumscribed; and that by placing the ligature nearer the heart, so as to diminish still more the extent of the circulation, a still larger part of the spinal cord might be destroyed without the circulation being interrupted. Legallois tied the aorta in rabbits in the lumbar region, and destroyed the lumbar portion of the spinal cord. In other cases, after decapitating the animal, he tied the carotids and jugular veins, and then destroyed the cervical portion of the cord, keeping up artificial respiration; and in still more barbarous experiments he removed the entire posterior half of the body after tying the great vessels. In all these cases the circulation between the heart and the ligatures was carried on for a longer or shorter time, and in many cases, according to Legallois' account, for more than three quarters of an hour.

The inference which Legallois deduced from his experiments was, that the sympathetic is not an independent nerve; that it is not merely connected with the spinal cord, but that it arises from it, and that it is the peculiar character of this nerve to place all parts to which it is distributed under the motor influence of the whole spinal cord. The committee appointed to examine Legallois' statement believed that these experiments solved all the difficulties which had before existed respecting the motion of the heart,—for instance, the influence of the passions on the heart, its independence of the will, and the persistence of the circulation up to the time of birth in anencephalous or acephalous monsters.

Dr. Wilson Philip,* however, has shown that the experiments of Legallois have not explained the whole relation between the brain, spinal cord, and sympathetic nerves. When an animal is deprived of voluntary motion and sensation by a blow on the occiput, respiration ceases, but the heart's action still continues, and may be supported for a long time by keeping up artificial respiration. If the spinal cord and brain are now wholly removed by the knife, the heart nevertheless still continues to beat, though feebly; and even when the spinal marrow and brain are destroyed by a hot wire, the heart's action generally continues. Hence Wilson Philip is led to a conclusion the very opposite of that of Legallois,—namely, that the heart's action is essentially independent of the brain and spinal marrow; although, as his experiments seem to show, the influence of both brain and spinal marrow has a great share in the sympathetic affections of the sympathetic nerve and heart.

Dr. Philip, having laid bare the spinal marrow and brain, and dropped

* Inquiry into the laws of the vital functions.

some alcohol upon them, the motion of the heart was increased; and in the most marked degree when the spirit was applied to the cervical portion of the spinal marrow, most feebly when it was applied to the lumbar portion. Opium and decoction of tobacco had the same effect. The stimulant effect of the opium and tobacco was evidenced before the narcotic influence; the motions, from being accelerated, gradually became slower. These stimulants still exerted their influence through the medium of the brain and spinal cord on the viscera when their application in this manner had ceased to have any effect on the voluntary muscles. Dr. Marshall Hall however states, that in his experiments neither opium nor alcohol produced acceleration of the circulation; and that poisoning with opium, at the same time that it produced tetanus, put a stop to the circulation. Dr. Wilson Philip infers that the heart through the medium of its nerves stands in relation with all parts of the brain and spinal marrow,—while individual voluntary motions are connected only with individual parts of the brain and spinal cord. Wilson Philip has also observed that the influence which destruction of the brain and spinal cord exerts upon the sympathetic nerve, and the viscera to which it is distributed, depends very much on the mode in which the operation is performed. If the brain is destroyed by cutting out single parts, if the whole brain is removed, or if the spinal cord is slowly destroyed by a hot stilet, the heart continues to beat for a long time, although more feebly than natural; but if the destruction is performed quickly, and as it were by crushing, the action of the heart is immediately stopped. Thus, when the brain of a living frog was crushed by the blow of a hammer, the heart immediately performed a few quick and feeble contractions, and then lay quite motionless for half a minute, and its action then returned, but feebly. The spinal marrow was now quickly destroyed with violence, and the motion was again interrupted for a time; the contractile power however was gradually recovered. Clift saw the heart of a carp continue to beat eleven hours after destruction of the spinal cord.

The conclusion that Flourens deduced from his experiments on fishes is, that the action of the heart depends solely on the respiration, and that it ceases when the respiratory movements are put an end to by injury of the portion of the nervous centre on which these motions depend; and that in fishes, the respiratory movements of which depend on the medulla oblongata only, respiration, and consequently the circulation, continues after injury of the spinal cord. Dr. Marshall Hall* has, however, seen the circulation in fishes endure for a very long time after destruction of the medulla oblongata. He nevertheless allows that the heart is in some measure dependent on the spinal cord and brain.†

* Essay on the circulation.

† On this subject consult Treviranus, Biol. iv. 644. Clift, Phil. Trans. 1815,

If the experiments of Legallois, Philip, and others, are taken into consideration, together with the facts already known, namely, that the heart when removed from the body still continues to beat for a long time, particularly the heart of reptiles, amphibia, and fishes; that depressing affections of the nervous system weaken the force of the heart's action; and that, with nervous fainting, feebleness of the circulation is combined; the following results may be deduced from them:—1. That the brain and spinal marrow have a great influence on the motion of the heart; that its movements may, through their agency, be accelerated or retarded, depressed or invigorated. 2. That the heart's action, however, still continues for a certain time after simple removal of the spinal cord and brain from the body. Flourens observed that pulsation of the carotids continues for more than an hour in rabbits under these circumstances, artificial respiration being kept up. That the heart's motions, however, are much feebler, and the circulation is not maintained perfectly, for any long period. 3. That even when the heart is cut from the body, and consequently separated from the greatest part of the sympathetic nerve, its contractions still continue for a short space of time.

The heart is not so much dependent on the influence of the brain and spinal marrow that the removal of these organs immediately annihilates its power of motion. The cardiac nerves, under such circumstances, still retain a portion of the motor influence, and even the small part of these nerves which can be contained in a heart cut from the body still retains sufficient nervous power to enable the organ to continue its motions for a short time. But the brain and spinal marrow must nevertheless be regarded as a principal source of the nervous influence; for their destruction enfeebles the heart's action to such a degree, that, although it is continued for a considerable time, its force is not sufficient to keep up the circulation. The only mode of ascertaining the degree in which the heart is subject to this influence is that adopted by Nasse. He measured the height of a stream of blood which issued from a divided artery in the normal state, then destroyed the spinal cord or single parts of it, and now found that the height of the stream of blood had in a few minutes diminished, and in a degree proportioned to the injury.

The sympathetic nerve, however, is certainly not dependent on the brain and spinal marrow in the same degree as the cerebro-spinal nerves. This is evident from the single fact, that in fishes the contractions of the heart continue for the space of half a day after destruction of the brain and spinal marrow.

Wedemeyer, Physiol. Untersuch. über das Nervensystem und die Respiration, Hannov. 1817. Nasse, in Horn's Archiv. 1817, 189. Flourens, Versuche über die Eigenschaften und Verrichtungen des Nervensystems; Leipz. 1824. Nasse, Untersuch. zur Lebensnaturlehre; Halle, 1818; which contains an elaborate review of the experiments of Legallois and a luminous statement of the whole subject. See also Lund, Physiol. Resultate der Vivisect. neuerer Zeit. Kopenh. 1825, 162.

Circulation in acephalous monsters.—In monsters in which brain and spinal cord are wanting, the circulation seems to be still more independent of the nervous centres, but the anatomy of these monsters is not at present known with sufficient accuracy for any conclusion with regard to the present question to be drawn from them. In hemicephalous monsters the brain has mostly been destroyed by hydrocephalus, and the same disease may also destroy the spinal marrow.

In acephalous monsters the heart also is generally, but not always absent; and the vascular system consists generally only of two systems of vessels connected, not by their trunks, but only by their capillaries, the umbilical vessels being branches of these trunks.* Winslow's case is the only one in which the umbilical vein was continuous with the arterial trunk, resembling that condition of the embryo in which the heart is merely the part at which the venous trunk makes a bend and is continuous with the arterial. It cannot be admitted that in the acephalous monsters without heart there had been no circulation. One point of the arterial stem may have had contractile power, and have thus supplied the place of the heart, which in the embryo at its earliest period had the form of a vessel. If a circulation really did exist, it could continue any length of time; and indeed since, in some of these cases, the spinal cord also was deficient, these monsters seem to prove that the circulation of the blood in their double system of vessels can be carried on without the aid of the brain and spinal cord, and consequently that the contractile parts of viscera, which are supplied by the sympathetic nerve, may be completely independent of the brain and spinal cord. Brachet† has collected all the accounts of acephalous monsters in which the spinal marrow also was deficient.‡ The case mentioned by Ruysch,§ in which an inferior extremity was connected with the placenta of a well-formed fœtus, is particularly remarkable. Emmert|| has described a product of conception which consisted almost entirely of an extremity hung to an umbilical cord, and contained vessels, arteries, and veins, and a short stump of spinal marrow.¶ There is no difficulty in explaining the circulation of the monster without heart and spinal marrow, in which its vessels are merely branches of the vessels of the umbilical cord of another fœtus, as was the case in the monster described by Rudolphi,** which consisted of a head only, and in the case which I observed myself of a head which was connected by arteries and veins with the umbilical vessels of a completely formed child.†† See also the case of the rudimentary

* Tiedemann, Anat. d. Kopflos. Missgeburt; Lanshut, 1813. † Loc. cit.

‡ See also Meckel, Pathol. Anat. i. Elben, De acephalis; Berol. 1821.

§ Thesaur. Anat. ix. p. 17. tab. i. fig. 2. || Meck. Archiv. vi.

¶ A similar case is described by Hayn, Monstri unicum pedem referentis descriptio anatomica. Berol. 1824.

** Abhandl. d. Akad. zu Berlin, 1816. †† Müller's Archiv. 1834, 179.

monster, of which Gurlt* has given a representation. Rudolphi, to explain the circulation in other monsters without heart, says that the blood of the mother passes to the fœtus through the umbilical vein, which is distributed through it like an artery, and that the arteries of the fœtus bring back the blood to the umbilicus and placenta.† This explanation, however, is very inconsiderate, for the vessels of the fœtus or placenta do not really communicate with those of the mother.

Influence of the sympathetic nerve on the heart's action.—Ackermann strangely asserted, without any grounds, that the sympathetic nerves of the fœtus is first formed. The very meritorious Rolando has also deserved censure in declaring the first traces of the vertebræ, at the side of the spinal cord in birds, to be ganglia of the sympathetic nerve.

Not only brain and spinal cord, but all the organs in their state of vital action, and consequently the whole system, react upon the sympathetic nerve through the medium of the nervous fibrils accompanying the blood-vessels, and excite its peculiar motor power. The constant source of the heart's contractility is, therefore, *primo loco* the motor power of the sympathetic nerve. But the maintenance of this power, and its excitement, is dependent not only on the brain and spinal cord, but probably on the vital stimulus transmitted by all the organs of the body through the medium of the nerves accompanying the vessels to the central portions of the sympathetic. Hence it is that a local disease is able to excite general feeling of illness in the whole body, and a very violent local disease can affect the heart's action and the pulse.

The modifications which the minute radicles of the sympathetic in any part undergo from violent local disease, and the reaction of these modifications on the central parts of the sympathetic system,—the cardiac nerves and the plexuses,—as well as on the brain and spinal cord, seem to have a main share in the phenomena which we call fever.

No observations have at present been made on the influence of particular portions, or regions of the sympathetic nerve, on the action of the heart. The only facts bearing on this point are those ascertained by Pommer,‡ who found in fifteen experiments that the division of the sympathetic in the neck had generally no important consequences. Several cerebral nerves being intimately connected with the sympathetic nerve, and the nervus vagus in particular having an essential share in the composition of the cardiac plexus, it would be very desirable to know, also, what influence these nerves exert on the heart's action. Emmert observed that division of the nervus vagus produces but very slight disturbance in the circulation; and Bichât and Legallois with justice remark, that the effects produced, which are by no means considerable, on the

* Pathol. Anat. 2 Bd. tab. 16, fig. 1—4.

† Encyclop. Wörterbuch der med. Wissensch. i. 226.

‡ Beiträge zur Natur-und Heilkunde; Heilbronn, 1831.

heart's beat, cannot with certainty be ascribed to the division of the nerve, since the mere pain and fear produced by the operation might give rise to them.

CHAPTER IV.

OF THE INDIVIDUAL PARTS OF THE VASCULAR SYSTEM.

Of the Arteries.

The middle coat of arteries is composed of flat fibres and bundles of fibres, which surround the vessel in a circular direction, are not muscular in their nature, and do not exist in veins. It is to these fibres that the arteries owe their great elasticity, or the property of contracting to their original diameter after being distended. Their elasticity is a physical property, and is preserved for a considerable period after death,—in fact, until decomposition ensues. It is by virtue of the same fibrous coat that arteries, even when empty, do not collapse, but remain of a cylindrical form, and that they are enabled to adapt themselves to very different degrees of fulness.

Cause of the pulse.—By each contraction of the ventricle a fresh portion of blood is propelled into the aorta, and the rapidity and force of the circulation in the arteries is increased. The periodic acceleration of the motion of the blood in the arteries thus produced was proved by Dr. Hales: having introduced a tube into an artery, he observed that the blood rose one inch, or even several inches, in the tube at every beat of the heart. The blood not being able to escape from the arteries as quickly as it is forced into them by the ventricle, on account of the resistance it experiences in the capillaries, necessarily exerts a pressure on the elastic coats, and thus gives rise to what is called the pulse. The pulse being dependent on the contraction of the ventricle, is, in general, synchronous with it. In consequence of the pressure exerted by the blood, the coats of the arteries become extended at each systole of the heart, while, during the diastole, they recover their former state by virtue of their elasticity. The extension of their coats takes place both in length and in the direction of their diameter, but the elongation is by far the most considerable. A necessary consequence of their elongation is, that they change their position and become curved; but they straighten themselves and recover their original situation when the ventricular contraction has ceased. Rudolphi, Laennec, Arthaud, Parry, and Doellinger, denied that the arteries undergo any dilatation. We have, on the other hand, the authority of Bichât, Von Walther, Tiedemann, Meckel, Hastings, Magendie, and Wedemeyer, for its existence: and in the entire course of the pulmonary artery in the lung of the frog the dilatation, as well as the incurvation of the vessel, can be seen with the greatest distinctness. I have also witnessed it in the abdominal aorta of the frog, and once

quite satisfactorily in the aorta of the rabbit. The dilatation must, however, be less considerable than the elongation, for it is not always observed with distinctness.* Poiseuille,† indeed, has measured the degree of this dilatation of the arteries. His experiment was ingenious; he laid bare the common carotid of a living horse for the space of three decimeters, or about twelve inches, and passed beneath it a tube of white metal, open at one side, which he afterwards closed by means of a narrower portion, so as to complete the tube; he then stopped the ends with wax and fat, and filled the interior of the tube around the artery with water, by means of a glass tube which was connected with the metallic tube. At every pulsation the water rose 70 millimeters‡ in the glass tube, whose diameter was 3 millimeters, and fell again the same distance during each pause. The included portion of artery measured in length 235 millimeters, and contained the space of 2,106 millimeters square; now, since at every beat of the heart it increased $3 \times 70 = 210$ millimeters square in calibre, it follows that it was dilated about $\frac{1}{11}$ of its capacity.

The pulse in different arteries.—It was asserted by Bichât, and is commonly admitted, that the pulse is synchronous in all the arteries of the body, whatever their distance from the heart.

Weitbrecht, Liscovius, and E. H. Weber§ have shown, however, that this is not the case. The pulsation of the arteries near the heart is synchronous with the contraction of the ventricle. But at a greater distance from the heart the arterial pulse ceases to be perfectly synchronous with the heart's impulse, the interval varying, according to Weber, from one-sixth to one-seventh of a second. Thus the pulse of the radial artery even is somewhat later than that of the common carotid. The pulse of the facial, at about the same distance from the heart, is isochronous with the pulse in the axillary artery; while the pulse is felt somewhat later in the metatarsal artery on the dorsum of the foot, than in the facial artery and common carotid. Weber‖ has explained the cause of this difference. If the blood circulated in perfectly solid tubes, whose walls admitted of no extension, the impulse of the blood, driven by the ventricle into the arteries, would be communicated even to the end of the column of blood, with the same rapidity with which sound is propagated through this fluid,—much quicker, namely, than in atmospheric air; the pressure of the blood would be transmitted to the finest extremities of the arteries, with no perceptible loss of time. But, in consequence of the arteries admitting of some extension, particularly in length, the impulse given to the blood by the heart distends first merely

* See the Observations of E. H. Weber, Hildebrandt's Anat. t. iii. p. 67.

† Magendie's Journal, t. ix. p. 44.

‡ [A millimeter equals 0 03937 of an English inch.]

§ In the Treatise De pulsu non in omnibus arteriis plane synchronico.

‖ Adnotat. Anatom.

the arteries nearest to the heart. These, by their elasticity, again contract, and thus cause the distension of the next portion of the arterial system, which also, in its turn, by contracting, forces the blood into the next portions, and so on; so that a certain interval of time, although a very short one, elapses before this undulation, resulting from the successive compression of the blood, and the dilatation and contraction of the arteries, reaches the most distant branches of the arterial system. Weber compares this action to the propagation of the undulations that are produced by a stone thrown into a lake; in which case, likewise, the undulations are not transmitted with the rapidity of sound. The rapidity of the transmission of undulations in water twenty-three inches deep is, according to the experiments of E. and M. Weber,* five and a half Paris feet in a second. Bichât confounded the motion of the undulations in a river with the movement of the water itself, and believed the pulse to be produced, not by the progressive undulations, but by the impulse communicated at the same moment to all the arterial blood. The motion of undulations always depends on the oscillations transmitted from the point where the impulse is applied, and never on the progressive motion of the fluid itself. The water of an undulation rises and falls, but remains in the same place, while the undulation and oscillation is propagated onwards in successive portions of water. Thus it is that very light bodies on the surface of undulations rise and fall, it is true, but remain in the same spot, while the undulation is progressive.

For the transmission of the pulse a continuous column of blood is required; if the arteries were empty at different points, the transmission of the pulse, as Weber remarks, would be much slower, or quite interrupted; for the parts of the arteries which contain no blood must be filled by the current of the blood before the impulse could be transmitted onwards, and the velocity with which the blood itself moves is much less than that with which the impulse is propagated. Hence Weber explains the fact of the pulse, in an artery affected with aneurysm, not being synchronous with the heart's action, and with the pulse of other arteries; for the coagulum in the aneurysmal sac, or spaces in it which are not quite filled with blood, may impede the propagation of the impulse.

The *arterial pulse* then, we may conclude, *is the effect of the oscillations propagated along the coats of the arteries, and in the blood itself, from the impulse communicated to the blood by the heart.*†

Motion of the blood in arteries.—The elastic coat performs an important use, as Weber remarks, in rendering the motion of the blood continuous by reacting in the intervals of the heart's action on the blood forced into

* Wellenlehre. Leipsic, 1825, p. 188.

† Weber, Adnotat. anatom. et physiol. prolus i.

the arteries at each systole of the ventricles. The blood escapes from a divided artery in a continuous stream, although this stream is accelerated at intervals, and the periodic acceleration becomes less perceptible in proportion as the arteries diminish in size. Weber remarks, that in this respect the vascular system resembles the fire-engine; in which the water is made to flow in an uninterrupted stream by the elasticity of the air in the air vessel, which continues to act upon the water while the piston remits its pressure.* The action of the regulator of the bellows is the same. By ossification of the arteries this elasticity is lost, and a disposition to apoplexy, gangrene, &c. is the consequence.

Contraction of arteries in proportion to the volume of their contents.—By virtue of their elasticity, arteries possess the remarkable property of diminishing their capacity in proportion to the quantity of blood they contain, and in proportion as it escapes from them when divided; for this reason, when an artery is divided, the stream of blood which flows from it becomes gradually smaller. In a horse, which Hunter let bleed to death, he found that the aorta had contracted to the extent of more than $\frac{1}{10}$th of its diameter; the iliac artery $\frac{1}{6}$th; the crural artery $\frac{1}{3}$rd; and that arteries of the thickness of the radial in man were completely closed.† The more forcibly the heart acts, the more are the arteries extended, and the more blood do they contain in proportion to the veins. On the contrary, when the heart's action is feeble, the coats of the arteries are more able to resist the impulse of the blood; they become less distended, and, consequently, contain proportionally less blood than the veins. This is what takes place just before death, and it is one cause of the absence of blood in the arteries after death; they are, in fact, for the most part, not quite empty, but contain as much blood as they are able to admit in their most contracted state. The gradual diminution in diameter which I, as well as Parry and Tiedemann, have observed arteries which have received no injury to undergo during the dissection of a living animal, must be attributed neither to the stimulus of the air, nor generally to the vital contractility of the arteries; it is a necessary consequence of the diminished force of the heart's action under such circumstances.

The arteries are not muscular.—The old writers, and many recent physiologists, have erroneously regarded the contraction of the arteries which follows their dilatation as a muscular act, and have looked upon the fibres of the middle arterial coat as muscular fibres. The fibres of the elastic coat of arteries are distinguished from muscular fibres by chemical characters, as Berzelius has pointed out. The muscular substance is soft and lax, and contains more than $\frac{3}{4}$ths of its weight of water, while the arterial fibre is dry and very elastic: muscular sub-

* Weber, l. c. De utilitate parietis elastici arteriarum. Hildebrandt's Anatomie, iii. p. 69.

† Abernethy Physiol. Lectures, 224.

stance has the same chemical properties as fibrin of the blood, is soluble in acetic acid, with difficulty soluble in mineral acids, with which it forms compounds difficult of solution; while the arterial fibre is insoluble in acetic acid, but readily soluble in mineral acids, and its solution is precipitated neither by alkali nor by ferrocyanuret of potassium, which must happen if it contained fibrin. [Dr. Hodgkin has also observed that the fibres of the middle coat of arteries, when examined by the microscope, do not present the transverse striæ which are seen on muscular fibres.] Another remarkable difference is, that the property of contracting after extension is preserved by the arteries long after death, for several days even; and fluid impelled by jerks into the arteries of a dead animal produces the same phenomena of pulsation and of subsequent contraction as are observed in the living body.

The different arguments for the existence of the pretended muscular contractility of arteries, which have been adduced from comparative and pathological anatomy, are of no weight. The dorsal vessel of insects, and the principal, though not all the vascular trunks of the annelides,—for instance, the leech,—certainly contract by muscular force. But these parts are hearts; for we have already shown that in the lower animals, as in the embryo, the heart is nothing more than a dilated part of the vascular system endued with contractility. The acephalous monsters, also, in which the heart is almost uniformly absent, have been adduced in favour of the muscular contractility of arteries; for in these beings the circulatory system consists of two sets of vessels connected at two different points by a capillary system, namely, in the placenta, and in the organs of the body; but here the heart is merely reduced to the simple tubular form. In many cases, also, the vessels of the acephalous monster are simply branches of the umbilical vessels of a second perfect embryo.* The bulbus aortæ of fishes and amphibia contracts, it is true, quite distinctly. I have even seen the bulbus aortæ of the frog, when cut away with the aorta, contract as perfectly and distinctly as the heart itself. But this part is quite different from the aorta; it belongs to the heart, and is peculiar to those animals which, during their whole life, or during the first period of it, have a branchial circulation. The aorta of frogs beyond the bulbus does not possess a trace of contractility; and Spallanzani,† who otherwise contends against the muscular contractility of arteries, is quite wrong when he asserts that the descending aorta of the salamander continues to pulsate when dissected from the body. Dr. Marshall Hall thought he had discovered an artery passing over the great transverse process of the third vertebra in the frog and toad, which continued to pulsate after the heart had been removed. But in this he was mistaken; there is in this situation in these

* See page 197.

† De' fenomeni della circolazione. Modena, 1773.

animals a peculiar pulsating lymphatic heart,* which is not, however, connected with an artery, but with a vein. The oscillating motion of the blood after tying the aorta of the frog, when the blood alternately advances and retrogrades for a short distance, but without regularity, is also no proof of the muscular contraction of the arteries, although Dr. Marshall Hall adduces it as such. It is entirely the result of the elasticity of the arteries, and of the different mechanical impediments to the course of the blood. The vena cava of fishes close to the heart possesses muscular contractility, and, according to Nysten,† contracts on the application of galvanism; Wedemeyer‡ also observed this phenomenon both in warm and cold-blooded animals. Their observations are perfectly correct: I have seen the termination of the inferior, and both superior cavæ of the frog, and of the pulmonary veins and cavæ of young warm-blooded animals, contract regularly; the venous trunks of the frog continue to contract even after the removal of the heart and auricle. But the rest of the venous system exhibits no trace of contractility either when under the influence of galvanism or at other times. If Flourens has seen regular contractions of the large veins in the abdomen, they evidently must have been produced by the action of the lymphatic hearts which I have discovered in the frog, and which pump the lymph into the jugular and ischiadic veins. The caudal heart of the eel at the extremity of the caudal vein is contractile, but the vein itself not at all so. The arteries of the thoracic fins of the chimæra, according to Duvernay, and of the electric ray also, according to Dr. T. Davy, seem likewise to have accessory hearts.

It has been urged as an argument for the muscularity of arteries, that the pulse in corresponding limbs sometimes differs in strength; for example, in paralysis: but here there are other local causes present to explain this anomaly. In paralysed limbs the mutual vital reaction between the blood and the solids is diminished; they are lax and shrivelled, and often less nourished: while, on the contrary, in active congestion, the increase of the vital processes going on between the blood and the texture of the parts,—the increased organic affinity,—induces a greater flow of blood to the part, and a consequently stronger pulse. In inflamed parts, in which there is accumulation of blood and impeded circulation through the capillaries, the strength of the pulse is increased. But there is no credible authority for the assertion that the pulse ever differs in frequency in different parts, and it is inconceivable how writers in these days can repeat such fables without examining into their accuracy. The rapid expulsion of the blood when an artery is punctured between two ligatures is also merely the result of the elasticity of the coats. Lastly, it has been argued for the muscularity of the arteries, and their active participation in the motion of the blood, that the gan-

* See the section on the Lymph and the Lymphatic Vessels, chapter ii.

† Loc. citat. p. 351. ‡ Loc. citat. p. 47.

grena senilis occurs principally where the arteries are ossified. But Wedemeyer remarks, that the gangrena senilis sometimes occurs where the arteries are not ossified, and such a state of the arteries does not always produce gangrene, so that the gangrena senilis requires other causes for its production; and the old error, "cum hoc, ergo propter hoc" is of no weight.*

Not merely, however, are all these arguments for the muscularity of arteries without grounds, but there are also counter-arguments to disprove their muscularity. Berzelius justly remarks, that the strongest galvanic and electric stimuli, which produce contractions in all true muscular structures, excite not the smallest motion in arteries. Nysten† repeatedly instituted galvanic experiments on the aorta of criminals just beheaded, but did not perceive the slightest contraction; nor could he excite any contractions in the aorta abdominalis of fishes by means of galvanism. Bichât had previously performed similar experiments with the same results; and Wedemeyer also has always failed to produce contractions in the carotids and thoracic aorta of many animals with a galvanic pile of fifty pairs of plates. I have myself made frequent experiments, with the aid of galvanism, to determine this question; and neither in frogs, with feeble or powerful degrees of the galvanic influence, nor in mammalia,—for instance, rabbits,—with a pile of from sixty to eighty pairs of plates, have I been able to produce the slightest trace of contraction of the arteries. It has been remarked by Bichât and Treviranus, that the heart also is insusceptible of the stimulus of galvanism; but Humboldt‡ observed just the contrary. And Pfaff, J. F. Meckel, and Wedemeyer, have detected this irritability in the heart in a marked degree. I have myself, with a single pair of plates, excited contractions not only in a frog's heart which had ceased to beat, but have also produced immediately most brisk contraction in the heart of a dog, which had also ceased to pulsate.

Mechanical irritation has as little effect as galvanism in producing contraction of the arteries. The application of chemical irritants, such as mineral acids, and muriate of lime, certainly gives rise to constrictions in arteries; but it is by producing a chemical change in their texture,—in many cases, by extracting a part of the water which they contain;§ so that this contraction by no means tends to prove their muscularity. The irritability of the muscles in mammalia never endures more than three quarters of an hour after death, while the contraction of the arteries on the application of chemical substances can be produced after the expiration of several days; and other non-muscular parts, such as the skin, are also susceptible of it. Zimmerman‖ observed contractions

* On all this subject consult Wedemeyer, loc. cit.

† Recherches de Physiol. et Pathol. chimiques. Paris, 1811.

‡ Ueber die gereizte Muskel-und Nervenfaser, 1797. i. 340.

§ See Hildebrandt's Anat. t. iii.

‖ De irritabilitate. Gött. 1751.

in fat on the application of sulphuric acid. Tiedemann and Gmelin* observed that sulphuric acid caused arteries to contract which had been preserved a year in spirit. Hot and boiling water, also, as Wedemeyer† remarks, even on the fourth day after death, produces in the human skin a contraction and curling very similar to muscular contraction; and we can with acids cause similar contractions in muscular fibres which have long lost their irritability, in the peritoneum, and in skin. All this proves that most animal tissues, without distinction, whether they possess muscular contractility or not, may, both in a living and in the dead state, exhibit contractility on the application of chemical irritants, from the operation of chemical affinities. These contractions, however, are altogether different from muscular contractions, which can no longer be induced when the parts have lost their vitality, and are excited not merely by chemical, but also distinctly and quickly by mechanical irritants, and by galvanism. Dr. Hastings‡ was in error when he imagined the contractions produced by chemical agents to be muscular in their nature; and also when he failed to recognise that the true cause of the contraction of the arteries, which follows their dilatation or pulse, is the elasticity of the coats,—the same property which produces in arteries injected with fluid by jerks after death, as well as during life, all the phenomena which are attempted to be explained by a mere assumption.§

Insensible vital contractility of arteries.—From all these facts it results that the circulation is in no way dependent on periodic muscular contractions of the arteries; and that the diminution of diameter of the arteries after their extension by the impulse of the blood forced into them is an effect of their elasticity only. It had hitherto been doubtful whether the narrowing of arteries observed in arresting hemorrhage from them, in exposing them to the air, and in the operation of torsion, is wholly and solely an effect of elasticity, or whether, in addition to this, they possess a vital property of gradual, not periodic, contraction, —*tonus.* This is admitted by Parry, Weber, and Tiedemann; the latter believes it to exist also in the trunks of the lymphatics. It had not, however, been actually observed until Schwann made his experiments by the application of cold water to the mesentery of the frog and rana bombina. After having extended the mesentery under the microscope, he placed upon it a few drops of water, the temperature of which was some degrees lower than that of the atmosphere. The contraction of the vessels soon commenced, and gradually increased, until, at the expiration of ten or fifteen minutes, the diameter of the canal of an artery

* Versuche über die Wege, &c. 68. † Loc. cit. p. 75.

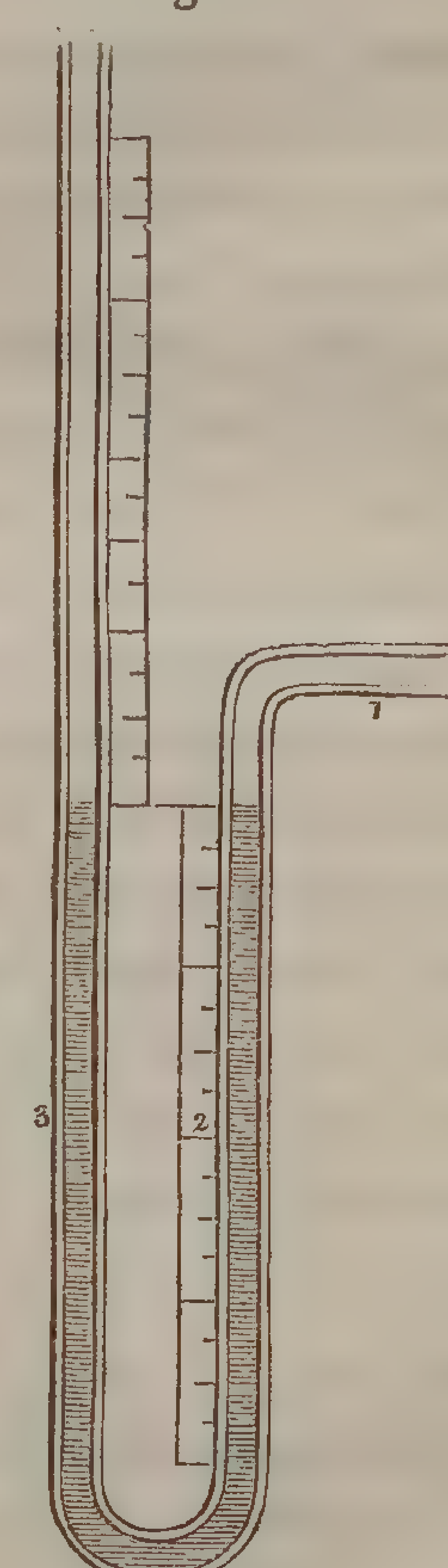
‡ On Inflammation of the Mucous Membranes. London, 1820. Translated into the German by Busch. Bremen, 1822.

§ See also the remarks of Dr. Parry on the arterial pulse. Bath, 1816. Translated into the German. Hanover, 1817.

in the mesentery of a toad, which at first was 0·0724 of an English line, was reduced to 0·0276. The diameter, therefore, was reduced to $\frac{1}{2}$ or $\frac{1}{3}$; the area, consequently, to $\frac{1}{4}$ or $\frac{1}{9}$ of its previous dimensions. The arteries then dilated again, and at the expiration of half an hour had acquired nearly their original size. By renewing the application of the water the contraction was reproduced; in this way the experiment could be performed several times on the same artery. The vital property of tonicity, which gave rise to these phenomena, will very well explain the partially empty state of the arteries after death; for the arteries, after a certain time, must lose the vital power of gradual contraction by which they had expelled their blood, and would again dilate, retaining merely their physical endowment of elasticity, which is not lost until decomposition takes place.

Force and rate of the blood's motion in the arteries.—The above enquiry, then, places it beyond a doubt that the only power by which the blood is moved in the arteries is the force of the heart's contraction. We have now to determine the degree of force which is thus exerted by the heart, and the force and rapidity of the blood's motion in different parts of the arterial system. Hales* was the first who made any observations on the height to which the blood rises in glass tubes introduced into different vessels: he observed that from the crural artery of the horse it rose 8 or 9 feet from the temporal artery of the sheep, $6\frac{1}{2}$; from the carotid artery of the dog, 4 to 6 feet; while from the jugular vein of the horse it rose only from 12 to 21 inches, in the sheep $5\frac{1}{2}$ inches, in dogs from 4 to $8\frac{1}{2}$ inches. We shall, however, on this subject have recourse chiefly to the accurate researches of M. Poiseuille.† M. Poiseuille made use of an instrument which he invented for the purpose. It was a long glass tube, bent so as to have a short horizontal portion, (fig. 15, 1,) a branch (fig. 15, 2,) descending at right angles from it, and a long ascending branch (fig. 15, 3). Mercury poured into the ascending and descending portions will necessarily have the same level in both branches, and in a perpendicular position the height of its column must be the same in both. If now the blood is made to flow from an artery through the horizontal portion of the tube

Fig. 15.



* Statical Essays. Translated into the German. Halle, 1748.
† Magendie's Journal, viii. 272.

into the descending branch, it will exert on the mercury a pressure equal to the force with which it is moved in the arteries, and the mercury will, in consequence, descend in this branch, and ascend in the other. The depth to which it sinks in the one branch, added to the height to which it rises in the other, will give the whole height of the column of mercury which balances the pressure exerted by the blood; the weight of the blood which takes the place of the mercury in the descending branch, and which is more than ten times less than the same quantity of quicksilver, must, however, be subtracted. M. Poiseuille calculated the force with which the blood moves in an artery according to the laws of hydrostatics, from the diameter of the artery, and the height of the column of quicksilver; that is to say, from the weight of a column of mercury whose base is a circle of the same diameter as the artery, and whose height is equal to the difference in the level of the mercury in the two branches of the instrument. To prevent the coagulation of the blood in the horizontal part of the tube, it was filled with a solution of carbonate of potash. According to Poiseuille, the force of the blood's motion in the larger arteries, for instance, in the carotid and crural arteries, and in the carotid and aorta, is equal; difference in size, and distance from the heart, being unattended by any corresponding difference of force in the circulation. The height of the column of mercury displaced by the blood was the same in all the arteries of the same animal. Poiseuille finds that the force of the blood in any large artery in a dog will support a column of mercury of 151 millim. or 6 inches, or a column of water of 6 feet 10 inches, English; in oxen (mare?)* a column of mercury of 161 millim. or 6 inches 4 lines, or a column of water of 7 feet 3 inches; in horses, a column of mercury of 159 millim. or 6 inches 3 lines: and, calculating from the former two animals, in the mean a column of mercury of 156 millim. or 6 inches 1½ line, or a column of water of 7 feet 1 inch.†

Poiseuille concluded from his experiments, which seemed to prove that the force with which the blood is moved is the same in the most different arteries, that to measure the amount of the blood's pressure in any artery of which the calibre is known, it is necessary merely to multiply the area of the vessel by the height of the column of mercury which is already known to be supported by the force of the blood in any part of the arterial system. The weight of such a column of mercury will represent the pressure exerted by the column of blood. For example,

* [M. Poiseuille does not mention the ox in the paper referred to.]

† [These numbers, if intended as the mean of the results given in M. Poiseuille's table, ought to be,

For the dog . . a column of mercury of	155·44	millim.
For the mare	164·36	—
For the horse	152·86	—
And the mean of the three will be . .	155·75	—]

Poiseuille estimates the diameter of the aorta at its origin, in a man of twenty-nine years, at 34 millimeters. Its area will therefore be 908·2857 square millimeters. Assuming now that the mean of the greatest and least height of the column of mercury found by experiments on different animals to be supported by the force of the blood, is equivalent to the height of the column which the force of the blood in the human aorta would support, we shall have the mean of 180 and 140 millimeters—consequently 160 millimeters—as the height of this column: 160 millimeters, then, multiplied by 908·2857=145325·71 cubic millimeters, will be the amount of mercury in the column, and the weight of this quantity of mercury,—namely, 1·971779 kilogrammes, or 4 lbs. 3 drs. 43. grs., [about 4 lbs. 4 oz. avoirdupois]—will indicate the static force with which the blood is impelled into the aorta. By the same calculation, the force of the circulation in the aorta of the ox [mare?] is found to be 10 lbs. 10 oz. 7 drs. 61 grs. [about 11 lbs. 9 oz. avoirdupois]; in the radial artery 4 drs.

Influence of respiration on the motion of the blood in the arteries.—Poiseuille perceived, by means of his instrument, what Haller and Magendie had already observed, namely, that the strength of the blood's impulse is increased during expiration; in which act the chest is contracted, and the large vessels in consequence compressed. The column of mercury in his instrument rose somewhat at each expiration, and fell during inspiration. M. Poiseuille found that the rise and fall of the mercury is the same in arteries, the distance of which from the heart is different, and that in ordinary tranquil respiration it amounts to from four to ten lines. The increase of the blood's impulse by expiration is in many persons so great, that the pulse at the radial artery becomes imperceptible when inspiration is long continued, and the breath held. This is the case with myself, and it in some measure explains the fable of persons possessing the power of altering the action of their hearts at will.

Effect of anastomoses on the motion of the blood in the arteries.—It was formerly believed that the angles at which the branches of vessels are given off, according as they are obtuse or acute, influence the rapidity of the blood's motion; the obtuse angle being supposed to retard it. But Weber * remarks that this circumstance influences the rapidity of the motion of a fluid only when it meets with so little resistance in its progress that the sum of the impulses which it receives can give a determinate direction to its course; but that, when the resistance it experiences is so great that each fresh impulse is lost in overcoming it, the angles at which the branches of the tubes are given off no longer have this effect. The fluid in the tubes in this case is everywhere exposed to the same pressure, and itself tends with equal force in all directions. The reason that the blood flows more slowly in the capillaries than in

* Hildebrandt's Anat. B. iii. p. 41.

the larger vessels is, that the aggregate capacity of the small vessels is greater than that of the vessels from which they arise. The causes which tend to diminish the rapidity of the circulation generally are not so much the frequent anastomoses of the arteries as the constantly increasing friction between the blood and the parietes in the small vessels. Anastomoses facilitate the distribution of the blood. When two arteries anastomose, branches may arise from the anastomosing vessels, or from the communicating branch itself. In the first case, the communicating branch, as far as can be observed with the microscope, is traversed in the direction which offers the least resistance, and the blood is conveyed into that vessel whose capacity is great enough to receive the blood of two vessels at the same time. In such cases, however, the anastomosis is traversed always in one direction. If the anastomosis itself gives off a branch, the blood flows either from two sides at the same time into this branch, or in one direction only. During life, the direction in which the blood flows in anastomoses must vary very much, according as accidental pressure affects the part.

Of the Capillaries.

1. *Structure of the Capillaries.*

Definition of the term "capillaries."—In all organic textures the transmission of the blood from the minute branches of the arteries to the minute veins is effected by a net-work of microscopic vessels, in the meshes of which the proper substance of the tissue lies. This is the appearance presented by all parts finely injected; and it can be seen during life, by the aid of the microscope, in any transparent parts,—such as the web of the frog's foot, the lungs and urinary bladder of the frog, the tail of the tadpole, the incubated egg, young fishes, the gills of the larva of the salamander, the wings of the bat, and the mesentery of all vertebrata, and, as I have pointed out,* even in some opaque textures of the larva of the salamander by means of a simple microscope. The ramifications of the minute arteries form repeated anastomoses with each other, and these anastomoses terminate at last in a continuous net-work, from which, on the other hand, the venous radicles take their rise. The reticulated vessels, connecting the arteries and veins, are, on account of their minute size, called capillary vessels. The point at which the arteries terminate and the minute veins commence cannot be exactly defined, for the transition is gradual; but the intermediate net-work has, nevertheless, this peculiarity, that the small vessels which compose it maintain the same diameter throughout: they do not continue to diminish in diameter in one direction and enlarge in the opposite direction, like arteries and veins. This, however, does not justify us in admitting with Bichât, that the capillaries are a peculiar system of vessels, distinct from arteries and veins.

* Meckel's Archiv. 1829.

The size of the capillary vessels is proportioned to that of the red particles of the blood, and can be measured in parts finely injected. Their diameter varies from $\frac{1}{1000}$th to $\frac{1}{4000}$th, even to $\frac{1}{5000}$th of an inch; but in the mean is most frequently between $\frac{1}{3700}$th and $\frac{1}{1850}$th of an inch.

Table of the size of the capillaries in different injected parts.

Organ.	*Observer.*	*Diameter in fractions of an English inch.*
In the brain	E. H. Weber	$\frac{1}{4700}$
Human kidney	Müller	from $\frac{1}{2500}$ to $\frac{1}{1592}$
Ciliary processes	Do.	$\frac{1}{1754}$
Mucous membrane of large intestines	Weber	$\frac{1}{2794}$ to $\frac{1}{1851}$
Lymphatic gland	Do.	$\frac{1}{2794}$ to $\frac{1}{1851}$
Skin	Do.	$\frac{1}{1149}$
Inflamed membrane	Do.	$\frac{1}{3846}$ to $\frac{1}{1923}$

The capillaries in their natural state, when filled with blood, and when they are not indeed extended so as when injected, have been seldom measured. In the scrotum of a new-born child, where the cuticle could be removed, Weber found their diameter to be $\frac{1}{2986}$th of an inch. In very young animals the capillary vessels are larger than in the adult, thus corresponding in size to the red particles of the blood, which are also in part larger at the former period. No other elementary tissues are much more minute than the capillaries. The muscular fibres, the minuteness of which has hitherto been much overrated, measure, according to Prevost and Dumas, $\frac{1}{7477}$th of an inch in diameter. The primitive fibrils of the muscles of man are five or six times smaller than the red particles of his blood. The primitive nervous fibril in mammalia, according to my measurement, is from one-third to one-half the size of the red particles of the blood.

No other tubes in the body are so minute as the capillary vessels. The diameter of the biliary ducts of the liver and of the tubuli uriniferi, even where they are the finest, is several times greater than that of the capillary vessels.* All these different elementary tissues, glandular ducts, muscular fibres, and nervous fibrils are surrounded and connected together by a net-work of capillaries. The primitive fibres of muscles, and those of the nerves, are not themselves traversed by any blood-vessels, for they are smaller than the finest capillaries. In examining recent and well-injected specimens of these parts, no other capillary vessels are seen than those which are distributed in the interstices of the primitive fibres, and it is the same with regard to the minute ducts of glands. The capillary vessels of the kidneys run everywhere in the interstices and on the surface of the urinary ducts; but the

* For the measurement of different microscopic parts, see the section on Secretion, chapter ii.

ducts themselves, according to my observations, contain no blood-vessels.

The form of the capillary net-work is in general very uniform, and varies merely in the size of the meshes, or in their being elongated or not. In the capillary net-work of muscles and nerves the meshes are elongated in the direction of the primitive fibrils on which they are distributed. The remarks of Soemmering and Doellinger, and especially those of Berres,* with regard to the variety in the distribution of the minute vessels in the different tissues, are very correct; they do not, however, refer to the capillary vessels themselves, but to the minute arteries and veins which ramify and divide still farther, before forming the capillary net-work. Soemmering observes, that the mode of ramification in the small intestines resembles a tree which is not in leaf, in the placenta a tuft, in the spleen an asperge or sprinkling-brush, in the muscles a branch of twigs, in the tongue a hair-pencil, in the liver a star, in the testicle and in the choroid plexus of the brain a lock of hair, in the Schneiderian membrane a trellis-work. In the branchiæ the arteries and veins take the direction of the branchial lamellæ, the arterial current ascending on one side, the venous descending on the other. The form of ramification of the vessels of tendons, which are not immediately connected with the long twig-like vessels of the muscles, is, according to E. H. Weber, dendritic. In the cortical portion of the kidneys there are peculiar glomeruli of blood-vessels in the midst of the capillary net-work.† Huschke has very recently proved that the minute artery which enters one of these vascular ganglia, after making several convolutions, again issues from it, and then becomes continuous with the capillary net-work.‡ At the extremity of each of the villi which form the tufts of the human placenta, a minute artery becomes directly continuous with the minute returning vein. This can be seen distinctly in the water-salamander. Thus the mode of division of the minute arteries presents many varieties, while the capillary net-work itself differs merely in the size of the meshes, and in their more oblong or equal-sided figure. Of this I have been convinced in the course of my researches on the glands; for in these organs, however various the distribution of the minute ducts may be, the capillary vessels have always the simple reticulated form, and do not follow in their arrangement the distribution of the ducts. In the medullary portion of the kidneys, where the urinary tubuli are collected into pyramidal bundles, the small arteries, and, as I have recently more than once satisfied myself by injection, the veins also, run in the form of long straight vessels between the urinary ducts,

* Med. Jahrb. d. Österr. Staates. Bd. 14.

† See the section Secretion, chapter ii. and my work De Gland. struct. penit. p. 100, 101.

‡ Tiedemann und Treviranus, Zeitschrift für Physiol. 4 Bd. 1 H. p. 116, tab. vi. fig. 8.

and have commonly been mistaken for ducts injected from the blood-vessels; but even these straight blood-vessels give off capillaries which form elongated meshes, and, diminishing in size as they run from the cortical portion towards the mammella, terminate at last on the mammella itself, in a fine net-work surrounding the openings of the urinary ducts. In the same way the smaller branches of the blood-vessels run along between the muscular and nervous fibrils; but the capillary vessels themselves form here a net-work around the parallel fibres of the muscles and nerves, just as they do in the testicle around the convoluted tubuli seminiferi, and in the cortical portion of the kidney around the convoluted tubuli uriniferi. The small arteries in the branchiæ of the salamander also follow the mode of division of the branchial lamellæ, and terminate at the extremity of each lamella in descending branchial veins; but between the two vessels there is also a net-work in the smallest lamella, which Rusconi and others have overlooked, but in which I have actually seen the red particles of the blood circulating.

Number of the capillaries and size of the meshes in different parts.—The parts in which the net-work of capillaries is the closest, that is, in which the meshes are the smallest, are the lungs and the choroid membrane of the eye. In the iris and ciliary body, even, the interspaces are somewhat wider. The vascular net-work is also very close in the mucous membranes of the lungs, liver, and kidneys, and in the cutis vera. In the choroid of the turkey the interspaces are of the same size, or even smaller than the capillary vessels themselves. In the human lung the interspaces are, if anything, smaller than the tubes which form the net-work. In the human kidney, and in the kidney of the dog, the diameter of the injected capillaries, compared with that of the interspaces, is in the proportion of one to four, or one to three. The brain receives a very large quantity of blood, but the capillaries in which it is distributed through its substance are very minute, and less numerous than in some other parts, so that the blood must pass through it into the veins more quickly than in other organs. E. H. Weber found the diameter of the capillaries in the brain, compared with the long diameter of the meshes, in the proportion of one to eight or ten; compared with the transverse diameter, in the proportion of one to four or six. In the mucous membrane—for example, in the conjunctiva,—and in the cutis vera, the same observer found the capillary vessels themselves much larger than in the brain, and the interspaces narrower,—not more than three or four times wider than the vessels. In the periosteum the meshes were much larger.* The bones, cartilages, ligaments, and tendons are the parts which have the smallest number of blood-vessels and capillaries. At the line limiting muscle and tendon, the great difference in the vascularity of the two parts is very observable; the greater number of

* Weber in Hildebrandt's Anat. 3 Bd. p. 45.

the blood-vessels of the muscles are, according to Doellinger, reflected back again, and have no immediate connection with the scanty vessels of the tendons. Prochaska* observed the same relation between the free portion of the synovial membrane and that which covers the articular cartilages. I saw a very beautiful injected preparation of the cartilages of the trachea, larynx, and costal cartilages made by Fuchse in the museum of Fremery at Utrecht. The existence of vessels in the internal shining layer of the serous membranes has hitherto been doubtful; but some injections of the peritoneum by Bleuland, which I saw at Utrecht, make me hesitate to adopt Rudolphi's opinion, namely, that the vessels of serous membranes are situated in the subserous cellular tissue; and Schroeder Van der Kolk† has injections of the peritoneum, which prove indubitably that this membrane contains vessels.

Have the minute arteries open mouths?—It is still doubtful whether the vitreous humour and the substance of the cornea are supplied with capillaries. Microscopic observations and minute injections have shown that the capillary vessels are merely the fine tubes which form the medium of transition from arteries to veins, and that no other kind of vessel arises from them; that the minute arteries have no other mode of termination than the communication with the veins by means of the capillaries; in a word, that there are no vessels terminating by open extremities. It is the more necessary to demonstrate this fact, which minute anatomy has clearly shown, since Haller unfortunately adopted, and thus contributed to confirm, the crude notions of his predecessors regarding the open terminations of arteries. He admitted that arteries terminate in five ways: 1st, by openings on the surface of membranes; 2nd, in lymphatics; 3rd, in secreting canals; 4th, in fat; and, lastly, in veins. But in those times the secretion of mucus and fat could not be understood without presupposing the existence of open extremities of the blood-vessels. After Mascagni, Hunter, Prochaska, and Soemmering had contended with success against this hypothesis of the open termination of arteries, it still remained a matter of doubt whether there was not a communication between the blood-vessels and the secreting canals of the glands. My researches, however, on the structure of all glands, in which better auxiliary means have been had recourse to, such as the injection of the secreting canals themselves, the use of the microscope, and the history of the development of the embryo, together with similar observations by Huschke and Weber, have proved that no such communications exist in any secreting glands, and that the radicles of the secreting canals, however various their form in the different glands, are always closed at their radicle extremity. The existence of exhalent vessels also, which even Bichât admitted, and supposed

* Disquisitio Anatomico physiologica organismi humani; Viennæ, 1812; p. 96.
† Observ. Anat. path. 27.

to be open side-branches of the capillary vessels, is purely hypothetical. An exhaling membrane, such as the peritoneum, has merely reticulated capillary vessels spread out over a great superficies, and the fluids are exhaled into the cavities by permeating the substance of the organ itself; all animal textures being permeable to fluids by virtue of the pores which, though not visible, must necessarily exist even in the smallest molecules of the animal substance which are capable of being softened by fluids. It is owing to this porosity that when arteries are injected with a solution of size coloured with cinnabar, a colourless fluid exudes on the surface of the membranes, as was pointed out by Mascagni, the colouring particles not being able to pass through the pores.

Serous vessels, that is, branches of the blood-vessels which are too minute to allow the passage of the red particles, and which are traversed therefore merely by the lymph of the blood, may possibly exist, but they have not been demonstrated. In favour of this hypothesis those parts are adduced in which no vessels carrying red blood have hitherto been discovered, namely, the cornea, the capsule of the crystalline lens, and the vitreous body.

Parts in which existence of blood-vessels is doubtful.—The existence of vessels in the substance of the cornea is doubtful; they have never been injected. Nevertheless, penetrating ulcers and granulations are formed in the cornea, which can scarcely be conceived to occur without the agency of vessels. I have repeatedly seen, in calves of nearly the full time, vessels in the conjunctiva of the cornea, which contained red blood, and which could with a lens be traced more than a line over the margin of the cornea. Henle has injected and made drawings of these vessels: they measured from $\frac{1}{1319}$th to $\frac{1}{694}$th of an inch, and the finest twigs were not then injected; their trunks, which arose from a circular vessel that ran around the cornea, were even somewhat larger than this. The preparations of these parts I have in my possession. Professor Retzius has by means of injection been able to see the same thing in the adult animals. These vessels, belonging merely to the very surface of the cornea, prove at the same time that the conjunctiva is really continued over the cornea, which Eble denies.* It is well known that in inflammation the cornea contains vessels carrying red blood. I saw at Utrecht, in the possession of Schroeder Van der Kolk, a most beautiful injected preparation of a slightly inflamed eye, in which the conjunctiva as well as the aqueous membrane were injected. The posterior capsule of the lens even in full-grown animals contains vessels carrying red blood, derived from the branch of the arteria centralis, which traverses the vitreous humour to reach the posterior capsule. I have seen these vessels sometimes filled with blood in the fresh eyes of the calf and ox; Zinn saw

* See Henle, De membranâ pupillari aliisque membranis oculi pellucentibus. Bonnæ, 1832.

the same thing. Henle has shown that the vessels of the posterior capsule in the fœtus communicate with vessels of the zonula Zinni or corona ciliaris, and of the ciliary processes; and he has injected and given a representation of the communicating branches. In the embryo of mammalia the vessels of the posterior capsule are connected by a very vascular membrane, which I have discovered,—the membrana capsulopupillaris—with the vessels of the pupillary membrane. This new membrane is stretched between the inner border of the iris and the inner border of the corona ciliaris, or the border of the capsule of the lens, and contains numerous parallel longitudinal vessels, which pass from the iris and pupillary membrane to the corona ciliaris and posterior capsule of the lens. In the anterior capsule the vessels are extremely difficult to demonstrate. In inflamed eyes they are distinct both on the anterior and posterior wall of the capsule, as I saw in an excellent injected preparation of a cataractous eye in Schroeder Van der Kolk's collection at Utrecht. The zonula Zinni, or corona ciliaris, appears, from Henle's and Schroeder's injections, to be a vascular organ, and to be of great importance for the nourishment of the transparent humours.

I have not seen any injected vessels in the vitreous body. Schroeder had a preparation in which something like vessels were apparent; but they might be merely adherent colouring matter. Henle has also shown me a preparation of the vitreous humour, in which there was something resembling injected vessels; but it was not convincing. However, I do not despair of seeing this part also injected.

All these facts, however, render it very probable that even the cornea and capsule of the lens, to which vasa serosa have been hitherto ascribed, are really provided with vessels carrying red blood; and it is certain that the capsule of the lens of the eye of the ox, as well as the corneal conjunctiva in the fully developed fœtus of the sheep, are supplied with red blood. The vessels of the corneal conjunctiva are certainly infinitely less numerous than those of the sclerotic conjunctiva; there is the same difference between those two parts as between that part of the synovial membrane which is free, and that which covers the articular cartilages. E. H. Weber remarks, very correctly, that a single stratum of capillary vessels is not at all recognisable by the eye alone; the colourless appearance of the parts of which we have been speaking consequently does not prove that they contain no blood-vessels. The mesentery, also, in the space between the large vessels appears to the naked eye to be equally free from vessels, and transparent; but by the aid of the microscope capillaries become evident in it.

Have the capillaries membranous parietes?—The question whether the minute capillaries have membranous parietes is important. It has been the universal testimony of observers, from Malpighi to Doellinger, that

in living animals no membranous walls are discoverable by the aid of the microscope. Doellinger* regards the blood as fluid animal substance, the substance of the organs as solid blood. Gruithuisen saw the blood flowing in the free spaces between the acini of the liver in the frog: this is seen, according to my experience, much more distinctly in the liver of the larva of the triton, which alone I found adapted for the observation.† Wedemeyer doubted the existence of membranous parietes, when he observed the broad currents of blood and the small islets of solid tissue in the lungs of the salamander. C. F. Wolff, Hunter, Doellinger, Gruithuisen, Baumgaertner, Wedemeyer, Meyen, and Oesterreicher, also deny the existence of membranous parietes to the capillary vessels; while Leeuwenhoeck, Haller, Spallanzani, Prochaska, Bichât, Berres, and Rudolphi are of the contrary opinion.

The argument for the non-existence of membranous tubes, which Doellinger and Oesterreicher deduce from the development of new vessels, cannot be applied to vessels already formed; and more accurate researches appear, indeed, to refute altogether the hypothesis of the circulation of the blood in canals without membranous tubes. The facts that fluids injected into the arteries pass into the veins without extravasation, and that currents cross above and below each other without uniting, have already been adduced. The number of the currents, and indeed the smallness of the islets of solid matter between them in the pulmonary membrane of the frog and salamander also tend to prove that membranous tubes must exist; for these small islets would otherwise be themselves sometimes involved in the currents. But there are also direct means of proving the existence of the membranous tubes around the capillary streams. For this purpose we must select a very delicate parenchyma, which easily softens and dissolves in water, so as to leave behind the net-work of capillaries. In a piece of the cortical substance of the kidney of a squirrel which had been laid in water for a short time only, but long enough to have become softened, the capillary vessels which are interlaced around the tubuli uriniferi appeared to me, when I examined them by the microscope, to be independent parts. In the choroid, iris, and ciliary processes, the capillaries are still more evidently substantial independent parts. They can, however, be demonstrated most distinctly in an organ which Treviranus has discovered,—I mean the leaf-like organ in the cochlea of the internal ear in birds. C. Windischmann‡ concludes, from his dissections, that these laminæ are merely folds and wrinkles of a membrane which arches over the spiral plates of the cochlea. The membrane is extremely delicate and pulpy; its soft substance is however traversed by an extremely beautiful net-work of vessels, which Windischmann has injected from the carotid; it dissolves easily in

* Denkschriften der Akad. zu München, 7.

† See Meckel's Archiv. 1829.

‡ De penitiori auris structurâ in amphibiis, cum tab. iii. Bonnæ, 1831. Lips. apud Voss.

water, leaving the beautiful vascular net-work with the meshes empty.* In the uninjected state, also, the vascular net-work remains after the pulpy substance has been dissolved. In other parts, the parietes of the capillaries must be regarded merely as surfaces formed of the substance of the organs in a more condensed state, not as very substantial distinct membranes.

2. *Circulation in the Capillaries.*

As viewed by the microscope.—If the circulation in any transparent part of a living adult animal is examined by means of the microscope, the blood is seen to flow through the minute arteries and capillaries with a constant equable motion. In very young animals its motion, though continuous, is accelerated at intervals corresponding to the pulse in the larger arteries, and a similar motion of the blood is also seen in the capillaries of adult animals when they are feeble: if their exhaustion is so great that the power of the heart is still more diminished, the red particles are observed to have merely the periodic motion, and to remain stationary in the intervals; while, if the debility of the animal is extreme, they even recede somewhat after each impulse. These observations of Wedemeyer, which I must confirm as the result of all my experiments, are of great importance; for they prove that, even in the state of the greatest debility, the action of the heart is sufficient to impel the blood through the capillary vessels. The pulsatory motion of the blood in the capillaries cannot be attributed to an action in these vessels themselves, for when the animal is tranquil they present not the slightest change in their diameter.

It might be supposed that, even in the natural state, the blood flows in this pulsatory manner through the capillaries, and that the apparent regularity of its motion is attributable to the rapidity of the circulation, which, when viewed by the microscope, appears even greater than it really is; but the fact that the blood flows in an equable stream from the veins, proves that the effect of the impulses communicated to the blood is, in the natural condition, really lost in the capillary system.

The cause of the equable motion of the blood in the capillaries must be sought in the elasticity of the arteries. The elastic coat of the artery acts like the compressed air in the air-vessel of the fire-engine. During each pulsation it is distended by the blood forced into it, but during the intervals of the heart's action it contracts again so as to force on the blood, and convert its merely periodic motion into a continuous although periodically accelerated one; by the time that the blood reaches the minute arteries, the impulse given to the blood by each contraction of the ventricle is lost in thus dilating the arteries, while the continuous motion—the result of their elasticity—remains. During its course through

* See Windischmann, loc. cit. tab. ii.

the vessels, the circulation of the blood will necessarily be modified by the unequal obstructions that it meets with in the smaller vessels, causing it to be checked for a time in one vessel while it circulates more quickly through others; but in the capillaries themselves the pulsatory motion will no longer be perceptible. When an animal, however, is much weakened, and the propulsive power of the heart consequently diminished, the arteries become distended by less blood at each pulsation, and in their turn react with less force upon the blood. The cause, therefore, which in the natural state renders continuous the periodic motion of the blood, is not under these circumstances brought into action, and the blood moves forward only at the time of each beat of the heart, the effect of which is then perceptible in the capillaries. The oscillating motion of the blood in debilitated animals is said by Koch* to be independent of the heart's action. To both Wedemeyer and myself, however, it appeared to be wholly dependent on the contraction of the heart being too feeble to overcome the resistance offered by the capillaries; so that some part of the blood, in the intervals of the contractions, receded again, notwithstanding the presence of the valves.

The degree of resistance which the capillaries offer can be calculated from the results of the experiments instituted with that view by Hales and Keill. The mode which Keill adopted was to compare the quantities of blood which flowed in a given time from the divided crural artery and from the crural vein of a living dog. The quantity derived from the crural artery compared with that from the vein was in the proportion of $7\frac{1}{2}$ to 3, so that from these data the resistance to be overcome in the capillaries would seem to neutralise $\frac{9}{15}$ths of the force with which the arterial blood moves.

Hales† injected the mesenteric artery of a dead animal with water by allowing a column of that fluid $4\frac{1}{2}$ feet high to press into the artery, having previously divided the intestines along the line opposite to the insertion of the mesentery. The quantity of water which flowed from the divided capillaries amounted to one-third only of the quantity which escaped in the same time when the larger branches of the artery were divided; so that the resistance offered by the capillaries equalled two-thirds of the force with which the water was forced into them.

Rate of the capillary circulation.—To make a comparison of the rate of the circulation in the capillaries and arteries, we must take the mean rapidity of the blood's motion in these vessels at different times and in different situations; for in the arteries the velocity of the circulation is greater at the moment of the pulse than in the intervals of this act, and in the capillary system it is seen by the microscope to vary very much in different capillary vessels.

* Meckel's Archiv. für Anat. u. Physiol. 6 Bd. p. 216.

† Statical Essays.

If the area of all the branches of a vessel united was always the same as that of the vessel from which they arise, and if the aggregate area of the capillary system was equal to that of the aorta, or, in other words, if the aggregate capacity of the tubes through which the blood passes was the same in all the degrees of their ramification,—the mean rapidity of the blood's motion in the capillaries would be the same as in the largest arteries; and, supposing a similar correspondence of capacity to exist in the veins and arteries, there would be an equal correspondence in the rapidity of the circulation in them. It is quite true that the force with which the blood is propelled in the arteries, as shown by the quantity of blood which escapes from them in a certain space of time, is much greater than that with which it moves in the veins, but this force has to overcome all the resistance offered in the arterial and capillary system,—this resistance must indeed be overcome by the heart itself; so that the excess of the force of the blood's motion in the arteries is expended in overcoming this resistance, and the rapidity of the circulation in the arteries, even from the commencement of the aorta, would be the same as in the veins and capillaries, if the aggregate capacity of the three systems of vessels were the same.

But since the aggregate area of the branches is always greater than the area of the trunk from which they arise, the rapidity of the blood's motion will necessarily be greatest in the latter, and will diminish in proportion as the aggregate area of the vessels increases.

The motion of the blood in the capillaries is wholly dependent on the heart's action.—Many physiologists, believing that the power of the heart is not sufficient to propel the blood through the capillary system, have imagined the existence of other auxiliary forces, such as contractions of the capillaries themselves, or a spontaneous motion of the blood,—neither of which, however, has been demonstrated by direct observation. On the contrary, it is irrefragably proved, that the motion of the blood through the capillaries is effected solely by the action of the heart; for in animals, of which the strength is much exhausted, the impulse communicated to the blood by the ventricles is visible in the capillaries; and the flow of blood from a divided vein is accelerated during expiration, proving that the increased impulse given to the current of blood by the compression of the great vessels in the chest is also transmitted through the capillaries to the veins. The dependence of the circulation of the blood in the veins on the action of the heart is also proved by the following experiment of Magendie. He applied a ligature to the leg of a dog, the crural artery and vein not being included. The vein was then tied separately, when it was seen to become turgid below the ligature, with the blood returning from the limb; and, if it was punctured at that part, the blood spirted out in a full stream. When the crural artery was compressed, the flow of the

blood from the vein gradually ceased, but recommenced when the pressure on the artery was remitted. Poiseuille, by means of the instrument already described, measured the pressure of the blood in the portion of a vein most distant from the heart, and found it to be exactly proportioned to that of the blood in the arteries, increasing and diminishing according as the force of the blood in the latter vessels was greater or less.*

The differences of the blood's motion in different capillaries arise from mechanical causes.—Wedemeyer's description of the course of the blood in the anastomosing capillaries agrees perfectly with what I have observed. Sometimes, he says, the red particles flow rapidly from one current into a second, as if by attraction. In other cases the current which they join is very rapid; but they are arrested, as it were, in the collateral current, and only from time to time find means of entering. Sometimes a red particle is even thrown back out of the rapid current into the weaker stream, and is then again repelled. I have also remarked that the same anastomosing branch between two currents sometimes receives the blood in one direction, and sometimes in the other, and that variations of pressure, and position, and motions of the animal, are always the causes of these changes. All these variations in the capillary currents are then, just as in currents of water on irrigated land, merely the results of mechanical causes. In the most minute capillaries, which are not red, nor even yellow, but quite transparent, there is merely a single line of red particles separated by unequal intervals, and from time to time no red particles are seen in these colourless vessels; but I have observed no canals through which red particles did not occasionally pass, and which, therefore, deserved the name of vasa serosa; and Wedemeyer, who says he has seen such vasa serosa, himself confesses that some of the red bodies traversed them from time to time. The red particles do not rotate on their own axis while passing through the capillaries; in the frog they appear, for the most part, to move with the long diameter in the axis of the vessel, but frequently they are placed obliquely, and their position suffers many changes from the mechanical influence of the coats of the vessels; the red particles themselves are quite passive, and never present the slightest sign of spontaneous motion. Several observers have asserted, that, in passing through a narrow portion of the vessel, the red particles are sometimes compressed and thus elongated. I have never seen this occur; the observation may have been erroneous, and have arisen from the elliptic particle having been presented to the eye in different positions at different times.

All the red particles which are carried into the capillary system by the arteries are returned from it by the small veins; none are apparently

* Müller's Archiv. 1834, p. 365.

retained in the capillaries, at least in an animal which is not enfeebled. Doellinger and Dutrochet maintain that they have seen the red particles arrested in their course in the vascular canals, and become united with the tissue. I have myself, it is true, frequently observed this arrest of the red particles, particularly in enfeebled animals, and, formerly, thought it possible that the red particles of the blood might in this manner lose their mobility; but more accurate observations have convinced me that these stagnant globules are soon again set free, and that it is only in a state of extreme debility that a complete stagnation—or rather coagulation—of the blood occurs in the minute vessels: the occurrence of coagulation under such circumstances cannot, however, be supposed to explain the process of nutrition, being rather the very opposite of it. Not a single observer has confirmed the assertion of Doellinger relative to the nutrition which he supposed to take place by union of the globules with the tissue, and the observations which I shall adduce in another place render it very probable that nutrition is effected by a totally different process.

Self-propelling power of the blood.—Treviranus, Carus, Doellinger, and Oesterreicher have adopted the opinion of Kielmeyer, that the blood is endued with a power of self-propulsion, which they suppose to be exerted in the capillaries during life independent of the heart's action, and to continue after the latter has ceased. This opinion seemed to be confirmed by the observations of Wolff and Pander, who asserted that, in the chick, blood is formed in the area vasculosa, and moves from the periphery of the area vasculosa towards the heart, before the latter has pulsated. The latter part of this statement is not confirmed. Baer doubts its accuracy: it appeared to him that the pulsation of the heart is first seen, and soon afterwards the motion of the blood, in the space of the transparent area, and that the influx of the blood from the area vasculosa to the heart took place last of all.* Wedemeyer also has not been able to convince himself that the motion of the blood in the area vasculosa commences before the pulsation of the heart. The other arguments for the independent motion of the blood in the capillaries are derived from the continuance of the blood's motion in parts removed from the body. The idea of spontaneous motion in a fluid independent of attraction or repulsion from the sides of another object is itself inconceivable; but, even omitting that from consideration, the facts brought forward in favour of the hypothesis, although in part correct, do not appear to me to justify the conclusions deduced from them. There are two conditions under which the blood in the capillaries of a transparent part separated from the body may still be seen in motion by means of the microscope:—1. As long as the blood continues to flow from the

* Burdach's Physiol. ii. 261.

divided vessels. Thus, for ten minutes after separating the foot of a frog from the body, I could still perceive motion of the blood from the minute vessels towards the larger; that is to say, towards the openings of the divided stems. These movements, in my opinion, depend simply on the escape of the blood from the divided vessels, which by their elasticity contract to a less diameter than they had before while in the state of forcible extension. The narrowing of the vessels can, in fact, be perceived by the aid of the microscope. If the divided surface from which the blood flows is elevated, together with the leg of the frog, the escape of the blood ceases sooner, and after five or six minutes not the slightest motion is perceptible in the capillary vessels. Wedemeyer's* observations agree in most particulars with mine, only that he does not mention the space of time that the motions continue. 2. The second condition under which the motions are perceptible is, when the direct rays of the sun are allowed to fall on a moist part separated from the body. The surface of the part then becomes dry and wrinkled so quickly, that the change is perceptible to the eye. This causes a more rapid emptying of the capillary vessels, which, when the direct rays of the sun are transmitted through the part, is attended by a flickering appearance. Thus, in the wing of a bat removed from the body, a trace of this flickering motion of the blood will be perceived in spots even for many hours, but only at that part where the most intense rays of the sun are at the time shining through. The extraordinarily rapid shrivelling of the surface may be seen with the naked eye. If the part which is becoming dry is moistened again, the shrivelling, and with it also the flickering motion in the interior of the vessels, ceases for some moments, but is renewed as soon as the evaporation and drying recommences. Even after a day and a half had elapsed I could still see a flickering in the interior of the moistened wing when it was illumined by the direct light of the sun. Baumgaertner† observed the blood in the frog's foot continue in motion from three to five minutes after ligature of the artery, and attributed the motion to a reciprocal action exerted between the nerves and blood; it most probably arose from the contraction of vessels which had previously been distended; anastomoses also might give rise to such appearances. The ingenious experiments of Baumgaertner unfortunately do not clearly prove what they are intended to do. Moreover, according to my observation, the circulation in the capillaries generally ceases very quickly on the compression of the artery of the limb, when the spontaneous motion of the red particles ought certainly to be seen if it exists at all. Having destroyed the vitality of the heart of a frog by the application of liquor

* Ueber den Kreislauf des Blutes; Hannover, 1828; p. 233.

† Beobachtungen über die Nerven u. d. Blut. Freiburg, 1830.

kali caustici, I could, by means of the microscope, for some time perceive motion of the blood in the capillary vessels, but it depended probably on the compression of the blood by the elastic coat of the arteries which had previously been in a state of forcible distension. In one case the blood in the capillaries remained fluid above an hour, and from time to time advanced a little, then receded, was still, and then again moved. These motions were probably produced by the compression of the vessels by slight motions of the frog, or of a single set of muscles of the leg. I deny, therefore, the existence of a self-propelling power in the blood.

If the blood moves independent of the heart's action, it must be by virtue of an attraction exerted on it by the solid walls of the capillary vessels, which seems to be what Baumgaertner and Koch suppose. If this attraction of the blood by the capillaries and the organised tissue really took place, it might produce an accumulation of blood in a part, such as is seen in the phenomenon of turgescence; but we cannot conceive how such attraction could aid the circulation of the blood, for it would cause the blood to become stationary in the capillaries, unless it be again admitted that this attraction of the capillaries for the blood is exerted only while the blood retains its arterial character, and ceases when it has become venous. It is only by such an affinity that the capillaries could assist the circulation. The congestion of certain parts at particular times is, however, no argument for the existence of this auxiliary force, for in this congestion there is accumulation as well as attraction of the blood. Although the circulation of the sap in plants, effected by means of attraction only, shows us the possibility of the occurrence of a similar phenomenon in animals, still there are at present no direct observations which prove it in a conclusive manner.*

Vital turgescence of the blood-vessels.—Although it be denied that the circulation is in any way aided by an attraction between the blood and the capillaries, the existence of such an attraction or affinity may, nevertheless, be admitted in the instance of the "turgescence, turgor vitalis, or orgasm," which is observed to take place in certain parts of the body, independent of the action of the heart.† This condition of turgescence in animals is analogous to phenomena which are so evident in plants, such as the afflux of sap to the fruit-bud, which contains the impregnated ovum.

The mutual vital action or affinity between the blood and the tissues of the body, which is an essential part of the process of nutrition, is, under many circumstances, greatly increased; and an accumulation of blood in the dilated vessels of the organ is the result. It

* See the account of the circulation in the lower animals, pp. 155, 156.

† See Hebensbreit, De turgore vitali. Lips. 1795. The view which this author takes of the subject is very erroneous.

is seen, for example, in the genitals during the state of sexual desire, in the uterus during pregnancy, in the stomach during digestion, and in the processes of the cranial bones, on which the stag's antlers afterwards rest, during the reproduction of these parts. The local accumulation of blood, with the dilatation of old and the formation of new vessels, is, however, seen most frequently in the embryo, in which new organs are developed in succession by a process of this kind; while, on the other hand, other organs, such as the branchiæ of the salamander and frog, and the tail of the latter animal, become atrophied and perish as soon as the vital affinity which existed between the blood and their tissues ceases to be exerted.

The phenomena of turgescence have been supposed to be dependent on an increased action or contraction in the arteries. But arteries present no periodic contractions of muscular nature; and a persistent contraction of the arteries, unless it were progressive,—vermicular, as it were,—or aided by valves arranged in a determinate direction, would be quite inadequate to produce a state of turgescence in any part.

To explain the state of orgasm of the uterus during pregnancy, and of the bony processes which bear the antlers of the stag, we must presuppose the existence of an increased affinity between the blood and the tissue of the organ. This condition may be excited very suddenly, as is seen in the instantaneous injection of the cheeks with blood in the act of blushing, and of the whole head under the influence of violent passions; in both of which instances the local phenomena are evidently induced by nervous influence. The active congestion of certain organs, of the brain, for example, while they are in a state of excitement, is a similar phenomenon.*

If the organ which is susceptible of the increased affinity between the blood and the tissue, is, at the same time, capable of considerable distension, tumefaction and *erection* take place.†

* See the remarks of Bonorden, in Meckel's Archiv. 1827, 537; and of Wedemeyer, l. c. 412.

† *The principal erectile parts* are the penis, which presents the phenomenon in the highest degree, the clitoris and the nipples in females, and the appendages on the head of some birds,—such as the turkey, meleagris gallopavo. In the erectile structures the vessels are susceptible of great dilatation, and the veins very sinuous, forming very numerous anastomoses and plexuses; so that the capacity of all the plexuses, when dilated, exceeds beyond comparison that of the arteries and veins which convey the blood to and from them. In the undistended state, the same quantity of blood is sent to the extensile vessels as returns from them; but, during the state of erection, the blood is probably retained in them, in consequence of the affinity between it and the parietes of the vessels being increased.

When the part is supported by a strong fibrous tissue, lying in the intervals of the venous plexuses and connected with an external fibrous tunic, as is the case in the corpora cavernosa penis, it acquires, during the state of erection, great tension and firmness.

Injected

Contractility of the capillaries.—Many substances, such as those called astringents,—for example, alum,—seem to have the property of producing an approximation of the molecules of living animal matter—a conden-

Injected matters pass pretty freely from the arteries of the penis into the veins, particularly in the corpus spongiosum urethræ, and glans. Professor M. J. Weber has shown to me a series of beautiful preparations of the penis injected from the arteries. (Cuvier, Anat. Comparée, t. iv.; Moreschi, Meckel's Archiv. v. 403; Ribes, ibid. 447; Tiedemann, Meckel's Archiv. ii. 95; Panizza, Osservazioni Antropo-zootomico-fisiologiche. Pavia, 1830.) In the corpus cavernosum of the penis of the horse there are a number of pale red bundles of fibres lying among the anastomosing veins. These fibres, for the most part, run longitudinally, but they are connected by transverse bands. Viewed by the microscope, they do not present any resemblance to muscular fibres. By boiling in water for seven hours they yield no gelatine. Their solution in acetic acid is precipitated by ferrocyanuret of potassium. All we can conclude from this analysis is, that they do not belong to the cellular, tendinous, or elastic tissues.

I could excite no contraction in the fibres of the corpus cavernosum, by means of galvanism, in a living horse. Hence they would seem not to be muscular. (Müller's Archiv. 1834, p. 50; 1835, p. 26.)

The principal exciting cause of the erection of the penis is, as is well known, nervous irritation, originating in the part itself or derived from the brain and spinal marrow. When the spinal marrow of an animal is irritated, or destroyed with a hot wire, erection and emission of semen are produced. Congestion of the brain and spinal cord has the same effect, and it is from this cause that the above-mentioned phenomena are sometimes produced in persons hanged. The nervous influence is communicated to the penis by the pudic nerves which ramify in its vascular tissue. Guenther has observed that, after division of these nerves in the horse, the penis is no longer capable of erection. (Meckel's Archiv. 1828, p. 364.) The stallion on which the experiment was performed was led to a mare; he showed desire to cover, but no erection of the penis took place. On the following day the penis was swollen, but not in a state of erection.

It has been supposed by some French writers, Chaussier and Adelon, and, in Germany, by Stieglitz, (Pathologische Untersuch. i. 175,) that the afflux of blood is not the first step in the process of erection; that it is, in fact, the consequence of a spontaneous dilatation of the tissue. But to this it may be objected, that there is no known instance of active dilatation, and that artificial injection of the penis produces a state exactly similar to that of erection. Stieglitz, at the same time, supposes that the trunks of the veins may probably have the power of contracting so as to close their canal; but some experiments which I made on the vena dorsalis, in the dog and the ram, are directly opposed to this hypothesis. Krause (in Stieglitz's work, p. 186, and in Mueller's Archiv. 1837) attributes to the erectores penis the power of compressing the veins of the penis, and of thus producing erection. Houston, again, (Dublin Hospital Reports, 1830,) has described, in different animals, certain muscles situated between the penis and the arch of the pubes, arising from the descending branches of the pubes, and uniting with each other in the middle line over the vena dorsalis. I have never been able to find them. The erection may be strengthened, at its commencement, by a voluntary contraction of the muscles of the perinæum; but if the essential cause of erection is not in action, this effect is only momentary. The erectores penis can be contracted at will, but this action will not produce erection if the penis is previously lax.

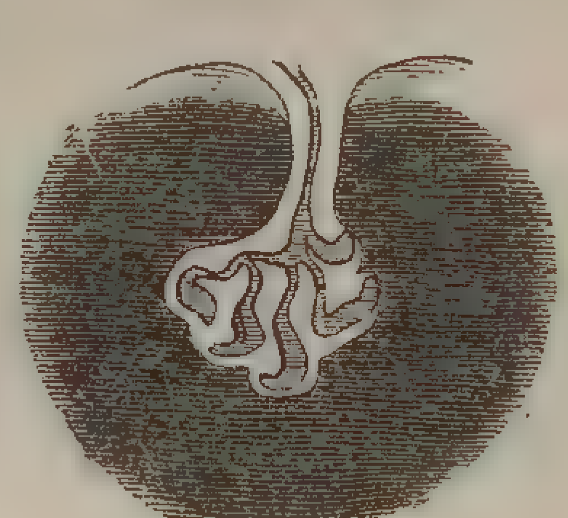
My discovery of the remarkable structure of the arteries of the corpora cavernosa penis throws new light on the phenomena of erection. The arteries of the corpora cavernosa have two sets of branches. The one set are the ultimate ramuscules, which

sation of the matter,—and thus a contraction of the tissues which it forms. It is to this effect on the capillaries and small arteries that we must attribute the action of such astringents, and of cold, in arresting hemorrhage from wounds.

There can be little doubt but that the effect of cold and astringents on the animal textures is much greater during life, for it is only during life that the peculiar state of the skin, called "cutis anserina," can be produced. If the "cutis anserina" arose simply from the blood being repelled from the surface, so as to leave the capillaries less turgid, the skin collapsed, and the follicles consequently more prominent, it would be produced by the same cause after death. It must, therefore, be dependent on a vital contractility of the skin; the follicles becoming more evident in consequence of the contraction of the surrounding skin. A similar contraction is produced in the prepuce by the action of cold, and in a still greater degree in the dartos. The vital insensible contractility here referred to is distinguishable from muscular contractility by the contraction of the part in which it is excited being gradual and feeble; moreover, muscular contractions are excited by the nervous stimulus under all circumstances,

terminate in the minute radicles of the veins, and are destined for the nutrition of the part. The other set come off from the side of the arteries, and consist of short, slightly curled branches, terminating abruptly by a rounded, apparently closed, extremity, turned back somewhat on itself; these are sometimes single; sometimes several arise by one stem, forming a tuft. (See fig. 16.) I have named them *arteriæ helicinæ*. They project into the venous cells, and are found principally in the posterior part of the corpora cavernosa, and of the corpus spongiosum urethræ. They are most distinct in man. Although no openings can be discovered in the coats of these free arterial excrescences, yet there is no doubt but that it is through them that the blood, which is ordinarily carried into the texture of the corpora cavernosa by the minute nutrient branches of the arteries, is in the act of erection poured directly into the venous cells and sinuses. When the arteria corporis cavernosi is injected with size and vermilion, the injected matter always fills the venous cells; and if it is afterwards washed from them, the arteriæ helicinæ will be seen injected. The means by which during life they are enabled to force blood into the cells, must be the increased attraction exerted between their coats and the blood by the nervous influence transmitted to them by the spinal cord, in consequence of which attraction an increased quantity of blood goes to them. This throws new light, at the same time, upon the mutual action of the blood and smaller vessels in other parts, and upon the phenomenon of active turgescence, or turgor vitalis. (Mueller's Archiv. 1834, p. 202, tab. xiii.) The blood is returned from the corpora cavernosa partly by small veins, running at the sides and on the surface of these bodies into the vena dorsalis, partly by deeper veins which issue from the corpora cavernosa at their root, and enter immediately the venous plexus, situated behind the symphysis pubis. The fact, then, that the vena dorsalis does not return the blood from the deep veins, shows that no pressure on the former vein alone can cause accumulation of blood in the penis. (See the article "Erection," by Mueller, in the Encyclop. Wörterbuch d. medicin. Wissensch.)

Fig. 16.



while this insensible contraction of the skin is not excited by its specific causes, such as cold and nervous affections, unless under such circumstances as at the same time determine a diminished flow of blood to the skin, which is probably dependent on some sympathetic influence on the heart's action; while all stimulants which induce a greater afflux of blood to the surface produce vascular turgescence, but not the phenomenon of cutis anserina. The insensible contractility displayed by the skin is probably possessed, in a greater or less degree, by all the soft parts which are organised; and there is no reason to suppose that the minute arteries and capillaries are not endued with it. Every stimulant, however, does not excite it. Thus the contraction of the small arteries and capillaries, which causes the arrest of hemorrhage in operations, is produced by the sudden action of specific influences,—such as cold; while other stimuli,—heat, for example,—might, by increasing the turgescence of the part, have quite the contrary effect. Wedemeyer states that no contraction is produced in the capillaries by the agency of galvanism, but that the blood becomes stagnated in them from coagulation taking place. In the small arteries, however, he perceived a distinct permanent contraction, which did not arise, he says, from the action of the acid developed at the positive pole, for it took place even when he applied the negative pole to the vessel. It might, however, in this case, be dependent on the action of the alkali developed at the negative pole.

Action of different substances on the capillaries.—Direct experiments to determine the action of different substances on the capillary vessels, by watching the changes produced by the application of these substances to the vessels of transparent parts, promised at first to increase considerably our knowledge of the action of the capillaries. But these experiments have left our knowledge of the subject in the greatest confusion. The most interesting observations are those of Thomson, Wilson, Hastings, Kaltenbrunner, Wedemeyer, and Koch. Two orders of changes are observed on the application of chemical agents to the small arteries, capillaries, and veins. In many instances,—for example, whenever common salt was applied,—dilatation of the capillaries ensued after a few minutes. In Wedemeyer's experiments, however, on the application of salt to the small arteries of the mesentery of the frog, contraction to the extent of $\frac{1}{5}$th of their diameter was the first effect, and this was followed by great dilatation. The application of ammonia was observed by Thomson to be followed by contraction of the vessels, with diminished rapidity of the circulation; while Wedemeyer and Hastings found it produce dilatation of the vessels with stagnation of the blood. Oesterreicher also observed dilatation follow the application of a weak solution of ammonia, while he found that concentrated matters produce

contraction of the vessels, and at last stagnation of the blood. Alcohol, according to Hastings, produced contraction of the capillaries: hot water had the same effect in frogs; the application of ice was also followed by contraction. Hastings remarked that these substances frequently caused contraction first, and afterwards dilatation. From the application of tincture of opium, tartaric acid, very dilute muriatic acid and alcohol, Wedemeyer obtained no constant result. In two instances only did alcohol cause retardation of the circulation, without, however, having excited distinct contraction in the small arteries. When dilatation of the vessels is produced, the circulation is generally at the same time retarded. Thomson is the only physiologist who has observed acceleration as well as retardation of the circulation accompanying dilatation of the vessels; and this was after the application of common salt. In vessels in which the substance applied has produced contractions, the rate of the circulation also varies, being sometimes retarded, sometimes accelerated.

The blood must, *cæteris paribus*, flow more rapidly in a contracted vessel; but if its fluidity had been diminished, or coagulation induced, by the substance applied, its motion will be retarded. In a dilated vessel, the circulation must, *cæteris paribus*, be slower: increased rapidity of the circulation in such a state of the vessels can be accounted for only on the supposition that dilatation from an external cause may diminish the friction in the vessel.

The explanation of the phenomena detailed above is at present quite impossible. The contraction in all these cases may be a vital action of the animal tissue, or it may be merely a chemical effect, which would be produced equally well on dead matter,—the substance applied may be supposed, for example, to extract from the tissue a part of its water. The dilatation of the vessels produced by certain substances may be a state of turgescence arising from an increased organic affinity excited between the blood and the tissue: it is, however, just as possible that it is merely the result of endosmosis. A salt when applied to a part permeates the tissue till it reaches the capillary vessels; an attraction is then exerted between the salt and the blood, which has a tendency to dissolve the salt, as the salt has a tendency to dissolve itself in the blood; the blood will in consequence of this affinity be arrested and accumulated in the capillaries; the capillaries will be dilated, and the circulation in them retarded. It is very probable that dilatation of the capillaries, when produced by the application of a salt, is dependent on endosmosis alone.

State of the capillaries in inflammation.—The results of the experiments detailed above appear, then, to admit of such different explanations, that they can be of scarcely any assistance in determining the state of the capillaries in inflammation. I shall therefore simply detail

the phenomena of this morbid process as they have been observed and described by Thomson,* Kaltenbrunner,† and Koch.‡

The minute vessels of an inflamed organ contain at every stage of the process an increased quantity of blood: at the commencement of the inflammation the blood flows into the capillaries in larger quantity than natural, circulates through them rapidly, and escapes from them into the veins without great difficulty; but in a more advanced stage of the disease the circulation becomes impeded, and stagnates in the distended capillaries; at first single vessels only, but at last all the capillaries of the part, are filled with blood, which is motionless, and very probably coagulated; at any rate it has undergone some change. Koch says that the colouring matter of the globules is dissolved by the serum in the inflamed part: this, however, is not probable, for in that case the fibrinous exudation would be coloured red. According to Koch, no new vessels are formed in inflamed parts; it must, however, be remembered that they are certainly developed in the fibrin effused during the inflammatory process. When the inflammatory congestion has attained its highest degree, in membranes which have a free surface, they pour out the dissolved fibrin of the blood. The fibrinous fluid or lymph coagulates on the surface of the membrane, forming pseudo-membranes. If the inflammation is situated in a part where there is no free surface on which this exudation can take place, the coagulable matter accumulates in the capillary vessels themselves. When the consequent arrest of the circulation takes place only in isolated tracts of the capillary system, while the circulation of the organ is carried on, though incompletely, by the other capillaries, the part is merely rendered denser in texture,—a state which is called hepatisation, when it occurs in the lungs; in other organs, induration. If the violence of the inflammation is so great that the circulation in the organ is completely arrested, and the blood in all the capillaries is not merely coagulated, but decomposed, while the tissue itself undergoes decomposition, such a part is said to be gangrenous, or mortified,—its vitality is lost. Thomson has observed, that the vessels in gangrenous parts are sometimes filled with coagulated fibrin, sometimes obliterated by the inflammatory process. Mortification ensues more readily when the nervous energy is diminished, and in paralysed parts.

If, after the congestion and effusion of lymph have taken place, the inflammation is still kept up, either by the persistence of the same causes, or by the accession of new, the tissue of the organ undergoes a peculiar change. The decomposed molecules of the tissue are separated

* Lectures on Inflammation, translated into German by Krukenberg. Halle, 1820.

† Exp. circa statum sanguinis et vasorum in inflammatione. Monach. 1826.

‡ Koch has given a review of the subject, with original experiments, in Meckel's Archiv. Bd. vi.

in the form of pus,—a matter consisting of globules larger than those of the blood. No one, not even Kaltenbrunner, has observed satisfactorily by the aid of the microscope the formation of pus. Cold-blooded animals are not adapted for this experiment; it ought to be instituted on mammalia,—on the wings of the bat, for example.

Nature of the inflammatory process.—In inflammation the phenomena are so far similar to those of vital turgescence, or orgasm, that the blood is attracted in increased quantity to the part, and escapes from it with difficulty. But the effects of inflammation show that it would be a great error to regard it as identical with increased vital action. In inflammation the function of the part is, in the first place, disturbed by the material change produced in it by the exciting cause of the inflammation; subsequently, nature makes an effort to repair this material change. In the reproduction of the antlers of the stag, in the phenomenon of erection, and in the turgid state of the uterus after conception, the turgescence is really combined with increased vital power, and the excitement and the vital energy in these cases advance to a certain extent *pari passu*, but in inflammation the material change is the only part of the process which goes on increasing. The appearance of turgescence which arises from the blood being attracted and retained by the inflamed tissue,—perhaps for the purpose of restoring them to their natural condition,—is gradually exchanged for that of gangrene. The latter state ensues as soon as the material change is so great that the tissues lose the power, which in the healthy state they possess, of preserving the vital properties of the blood, which then itself becomes decomposed in the vessels. Inflammation is produced by irritation of the capillaries, but itself consists neither in an increased nor in a diminished vitality. It is a peculiar state which may occur with the general vital powers in their normal state, or with these powers depressed; and which, in proportion to the degree of its developement, if in an important organ, always exhausts the vital powers, even if they were not previously enfeebled. It is in fact a mutual action, morbid in its nature, which is set up between the tissues and the blood, in consequence of the material changes produced in the part, and which is compounded of the original lesion of the part, of a local tendency to decomposition, and of a vital action striving to counterbalance the tendency to decomposition. The vital action of the part sometimes overcomes the morbid tendency, as is exemplified by a healing wound; sometimes it does not.

Influence of the nerves on the circulation in the capillaries.—Several physiologists have recently sought to prove that the nerves have a great share in keeping up the circulation in the capillary vessels. Treviranus and Baumgaertner have done most to support this theory. But although it is certain that turgescence of the tissues—their attraction of the nutritive fluid—is dependent on the influence of the nerves, it does

not necessarily follow that this influence should at all aid the circulation. The numerous experiments of Baumgaertner are far from being convincing. He himself confesses that many of them are not strictly conclusive; and, unless proofs are free from doubt, their number does not better establish the fact. Baumgaertner directed a strong galvanic current through the ischiadic nerve to the foot of a frog; the irritability of the nerve was destroyed, and in most cases the circulation in the limb was arrested. But here, by destroying the nervous energy of the part, the influence by which the coagulation of the fibrin is prevented was abolished; and, besides this, it must be remembered that galvanism itself will produce coagulation of the albumen in the blood. After destruction of the spinal cord and brain, Baumgaertner saw the motion of the blood in the capillaries become slower, although the heart continued to beat. But here, again, the motion of the heart itself was weakened; and experiments which rest upon an indefinite "more" or "less," are not proofs.

Treviranus asserted that division of the ischiadic nerve in the frog caused the circulation in the web of the foot to cease. But even Baumgaertner denies that this is the case if the web is kept properly moist.

The numerous experiments of Dr. Wilson Philip* also fail completely to establish the influence of the nerves on the circulation in the capillaries. The retardation or cessation of the circulation in the capillaries which he observed when opium or infusion of tobacco were applied to the brain and spinal cord, or when these parts were suddenly destroyed, was dependent on the effect which was produced simultaneously on the heart. Koch† also made an ingenious and simple experiment with a view to determine the same point. He amputated the leg of a small frog, and found that the motion of the blood in the capillaries of the web of the foot continued for three minutes only. He then, in another frog, divided all the parts of the thigh but the ischiadic nerve, by which he left the limb attached to the body; and he now perceived motions in the capillaries for the space of a quarter or half an hour. I have repeated this experiment, but not with the same result. The motion of the blood in the capillaries continued about ten minutes when the limb was completely separated from the body in strong frogs; and there was no difference in respect to time when it was left attached by the ischiadic nerve. In this experiment an error may be induced by the frog retaining the power of producing voluntary contractions of the muscles of the limb as long as the ischiadic nerve maintains its connection with the nervous centres. After each contraction of the limb, a slight motion of the blood in the capillaries is perceived; but the cause of this is evidently mechanical.

* Experimental Inquiry into the Laws of the Vital Functions.

† Meckel's Archiv. 1827, p. 443.

In the following experiment I avoided this cause of error. I laid open the spinal canal in a frog, and while my assistant, M. Hoevel, applied the wires of a simple galvanic circle to the posterior roots of the spinal nerves,—the irritation of which excites no contractions of the muscles,—I watched the circulation in the foot of the frog. At the moment when the galvanic stimulus was applied, no change was produced in the motion of the blood. This experiment, however, is not conclusive, for it may be the anterior roots of the nerves from which an influence on the circulation is derived.

From the facts which we have detailed, it appears most probable that the nerves do not really assist in carrying on the circulation in the capillaries, although it is certain that nervous influence is the principal cause of the accumulation of the blood in the capillaries of certain parts during the state of vital turgescence. The observation that in a frog much exhausted the impulses communicated to the blood by the feeble contractions of the heart are perceptible in the capillaries, proves that no other force than that of the heart is required to support the circulation.

Of the Veins.

Auxiliaries of the venous circulation.—The action of the heart is aided in accomplishing the circulation through the veins by the action of the *valves* with which the veins are provided, and which are so arranged that any intermitting pressure on the veins favours the motion of the blood towards the heart. Hence the want of proper bodily exercise must have an injurious effect on the circulation, if it were merely from the loss of the aid which the action of the muscles affords to the motion of the blood in the veins. The veins themselves, with the exception of the root of the vena cava and pulmonary veins, have no contractile power.*

Active dilatation of the heart.—Many recent writers, believing that the contractile power of the heart is insufficient for the completion of the circulation of the blood, ascribe some share in the blood's motion to a power of suction which they suppose to be possessed by the heart. They imagine that, after the heart has contracted, its cavities return to a state intermediate between dilatation and contraction, so as to give rise to a relative vacuum. The degree to which the heart dilates after its contraction, independent of being dilated by a fluid, can be but slight. But let us inquire how much effect is to be attributed to such a dilatation of the heart. During the contraction of the auricle, the great veins become more distended with blood, either on account of the reflux of a part of the blood of the auricle into them, or from that which they were pouring into the auricle being arrested in its progress. During the dilatation of the auricles the distension of the veins diminishes. This was observed by Magendie and Wedemeyer, and it is exactly what I

* See pages 170 and 204.

have myself witnessed in the dog. It is necessary to know this fact before forming an opinion on the following experiments. Wedemeyer and Guenther, having tied the jugular vein in a horse, made an opening into it between the ligature and the heart, and introduced a catheter, to which a bent tube had been cemented. The longer descending branch of the glass tube (two feet in length) was placed in a glass filled with water. At first the inspirations and the contractions of the heart were nearly simultaneous and of the same frequency,—namely, thirty in a minute,—and the coloured water rose suddenly two or more inches in the glass tube at the moment of each inspiration and pulsation, and sank again each time to its former level. The inspirations gradually became twice as frequent as the pulsations of the heart; and Wedemeyer and Guenther now observed for a long period, that the rise of the fluid did not take place at each inspiration, but at every beat of the heart, and consequently simultaneously with each dilatation of the auricle. This experiment seems to prove beyond doubt the sorbent power of the heart. This power is not, however, the principal cause of the blood's motion in the veins; for the fact, that large veins when divided continue to pour out blood from that portion of the vein which is distant from the heart, and connected with capillaries and arteries, proves that the propelling power of the heart's contraction extends to the veins; and Magendie has shown that the stream of venous blood from the lower end of a divided vein becomes stronger during each expiration; which proves that the effect of the compression of the arterial trunks which takes place during expiration extends to the veins; and it is evident that the force thus exerted is far inferior to that of the heart's contractions.

The circulation in fishes also shows that the passage of the blood through a system of capillaries does not destroy the *vis à tergo* with which it is propelled; for in these animals the heart sends the blood through two systems of capillaries; first through that of the branchiæ, from which it passes into the systemic arteries, which, as Nysten has shown, have themselves no contractile power; and afterwards through the general capillary system of the body. In all vertebrate animals, indeed, the *vis à tergo* derived from the heart is sufficient to propel the blood through the capillaries of the liver, after it has already circulated through the capillaries of the other abdominal viscera.

Influence of respiration.—Sir David Barry has recently given a new turn to these inquiries respecting the circulation in the veins. The heart, he says, when distended with blood, completely fills the pericardium; but, when it contracts, it no longer occupies the same space, and a partial vacuum ensues. To enable the auricles to fill this vacuum, the blood rushes into them from the great venous trunks. But Sir D. Barry attributes more importance to the effect of inspiration. During

inspiration, he says, a partial vacuum is formed in the thoracic cavity, and all surrounding fluid must strive to enter it to fill the vacuum; the atmospheric air rushes in through the trachea, distending the lungs in proportion to the dilatation of the thorax, and in the same way the fluids in the vessels of the body being subject to the pressure of the atmospheric air, will be forced into the cavity of the thorax and distend the trunks of the great vessels contained in it. But in consequence of a vacuum being formed in the pericardium at each contraction of the heart, the blood of the great venous trunks is drawn into the auricles to fill this vacuum; so that the afflux of blood to the cavity of the thorax during inspiration takes place principally towards the auricles. To prove the correctness of his theory, he performed the following experiment: he introduced one end of a bent tube into the jugular vein of an animal, the vein being tied above the point where the tube was inserted; the inferior end of the tube was immersed in some coloured fluid. He now observed that at the time of each inspiration the fluid ascended in the tube, while during expiration it either remained stationary, or even sank. When the tube was introduced into the pericardium itself, he observed the same ascent of the fluid.

Poiseuille has instituted some experiments to determine the same question, but in a more accurate manner. He employed the instrument described at page 207 (fig. 15). A solution of carbonate of soda was poured into the tube, filling both the perpendicular branches till it rose to a level with the horizontal portion; this point was the 0 of the scale. When the horizontal portion of the instrument thus prepared, is connected with the cavity of a vein, if any suction is exerted in the vein, a part of the fluid will be drawn out of the instrument, and its level in the great perpendicular branch ([3], fig. 15) will fall; if, on the other hand, any pressure is exerted by the blood in the vein on the fluid in the horizontal portion, the level of the fluid in the branch ([3]) will rise. The instrument was connected with the jugular vein of a dog; and it was observed that during expiration the fluid rose in the branch ([3]), and fell during inspiration; the rise at first equalled 3 inches 4 lines, the fall was 3 inches 6 lines below the previous level; afterwards the fluid ascended only 2 inches 4 lines, and fell 2 inches 9 lines below the level. During great muscular efforts, the ascent of the fluid at the time of expiration was as much as 5 inches 6 lines, or 6 inches 1 line above the level; and the descent during inspiration 9 inches 5 lines, or 9 inches 11 lines below it. These experiments, which on repetition afforded the same results, confirmed Barry's opinion that during inspiration the venous blood of the body is drawn into the venous trunks in the thorax. The effect of expiration, on the other hand, in repelling the blood, is prevented by the action of the valves, and by the pressure exerted on the blood in the veins by the muscles.

Barry, however, has estimated too highly the influence of inspiration on the motion of the blood. It is observable only in the large veins near the thorax. Poiseuille could not detect it by means of his instrument in veins more distant from the heart,—for example, in the veins of the extremities. The act of inspiration empties the large veins in the thorax, and less resistance is in consequence offered to the entrance of the blood from the other veins; but it cannot be the principal cause of the motion of the blood in the veins; and in the reptiles, which breathe by the movements of deglutition, in fishes, and in the fœtus, no movement of inspiration is performed. There can be no doubt, therefore, that the same power that moves the blood in the arteries, also effects its motion in the capillaries and its return to the heart through the veins; and that by the effect of inspiration on the great venous trunks, by the sucking action of the heart, and by the action of the valves, a part only of the resistance which opposes the course of the venous blood is overcome.

The changes produced in the motion of the blood by the contraction of the thorax during expiration, give rise to the tumefaction of certain parts. The vascular trunks are in expiration so compressed, that the blood is sent with increased force into the arteries, while the influx of blood into the right auricle is arrested. The consequence of this is not merely that the jugular veins become distended, but that even the brain is more fully injected with blood. In cases where a portion of the skull has been removed by the trephine, the brain is consequently in most cases seen to be elevated somewhat during expiration, and to collapse again during inspiration. Magendie declares that he has also observed this to take place in the spinal cord. In the natural state, the cranial cavity being inclosed by solid walls, no such movements of the brain can be caused by respiration, the brain cannot then alter its volume. All that has been advanced in favour of such a change of volume taking place in the natural state, is refuted by the physical impossibility of its occurrence.

The effects of impediment to the circulation in the larger veins are effusion of the watery and albuminous parts of the blood into the serous cavities and the cellular tissue. The fibrin is not effused. This may be explained perhaps by the circumstance that the fibrin is being constantly removed by the lymphatic vessels.

State of the vessels after death.—It is not rare to find blood in the arteries after death; for instance, such is the case in persons hanged, in those drowned, or suffocated by vapour of charcoal, also after inflammation, and in ossified arteries.* But commonly the arteries are found to contain proportionally less blood than the veins. It is the property of arteries, as is well known, to contract both in diameter and length, so as to adapt themselves, to a certain extent, to a diminished quantity of blood.

* Otto Path. Anatomie, i. . 343.

By virtue of this property of elasticity, the arteries at the moment of death force onwards the blood contained in them, while they assume the narrowed state in which they are afterwards found.* At a later period the quantity of the fluid in the vessels must be greatly diminished by the fluid part of the blood escaping through their porous coats, which like all animal tissues are susceptible of imbibition. Dr. Carzon† ascribed the absence of blood in the arteries after death chiefly to the action of the lungs. He supposed these organs to contract after the last expiration by virtue of their elasticity still further, so as to produce in the chest a vacuum, to fill which blood is drawn from the body into the large venous trunks. When he had opened the thorax of the animals while dying, he found that the arteries afterwards contained a larger quantity of blood than under other circumstances. But he has certainly overrated the elastic power of the lungs. Dr. Parry believed the empty state of the arteries to be the result of their tonic contraction,‡ which he supposed to take place immediately after death, so as to force their contents onwards into the veins, but to cease after a time, when the arteries again become dilated. Dr. Parry states that he has observed these changes in the diameter of the arteries after death. This explanation is more probable than that afforded by the unconfirmed hypothesis of an attraction which the capillaries are supposed to exert on the red particles of the blood in the arterial state, but not on those of venous blood.§

CHAPTER V.

OF THE ACTION OF THE BLOOD-VESSELS IN THE PROCESS OF ABSORPTION AND EXUDATION.

a. Of Absorption.

Before the discovery of the lacteals by Asellius in 1622, the office of absorption was ascribed to the veins; but after the discovery of Asellius, and when it was known that similar vessels existed in most parts of the body, they were supposed to be the sole organs of absorption. The fact of the lacteals becoming turgid with chyle soon after taking food, and the arrangement of their valves, which is such as to favour the course of the chyle and lymph towards the thoracic duct, and to prevent its motion in the opposite direction, are corroborative of the opinion that they perform the function of absorption. It has, however, at different times been remarked that the lymphatics cannot be the sole organs of absorption. The absorption of the osseous matter in the interior of bones in the formation of their cells, and the absorption of the

* See page 193.

† Inquiry into the causes of the motion of the Blood, pp. 97. 108. 117.

‡ See page 206. § See page 224.

alveoli of the teeth in old persons, are facts well known, and yet there are no lymphatics in bones. It is certain also that pus, portions of the lens, and of blood in the interior of the eye, become absorbed, and nevertheless no lymphatics have been discovered in the interior of that organ. Lastly, we need only instance the absorption of the yolk of the egg by the germinal membrane, in which no one will assert that there are lymphatics during the first days of incubation; if the invertebrate animals, which possess no lymphatics, did not sufficiently prove the possibility of absorption being performed without the agency of these vessels.

Do the capillaries absorb?—But it required a long course of experiments to establish the fact of the immediate absorption of matters into the blood without the aid of lymphatics. Magendie, Emmert, Mayer, Lawrence, Coates, Tiedemann, Gmelin, and Westrumb, have particularly distinguished themselves in this inquiry.

Delille and Magendie divided all the parts of the thigh of a dog except the crural artery and vein, leaving merely these vessels, which were dissected quite clean, and freed from their cellular coat, to maintain the connection of the limb with the trunk; two grains of a strong poison (the upas ticuti) were then inserted into a wound in the foot. The action of the poison was as rapid as if the limb had been previously uninjured. The symptoms began to show themselves in four minutes, and in ten minutes the animal was dead.

The same physiologists made a similar experiment on a convolution of intestine in a dog, in which the lacteals had been previously made visible by giving the animal a good meal. The intestine was tied at two points, with an interval of fifteen or sixteen inches; the lacteals of this portion of intestine were then tied each with two ligatures and divided. They satisfied themselves that no other lacteals ran from this part of the intestine, so that its only means of communication with the circulation were the arteries and veins. They now injected into the intestine two ounces of decoction of nux vomica, and retained it there by a ligature. Symptoms of poisoning ensued in six minutes.*

Magendie laid bare one of the jugular veins in a young dog of six weeks old, and isolated it from surrounding parts in its whole length, so that he could pass a card beneath it. He then applied freely to the vein a watery solution of spirituous extract of nux vomica. The symptoms of poisoning appeared before the fourth minute; when a similar experiment was made on an adult dog, the symptoms came on in ten minutes.†

Segalas‡ has repeated these experiments in a different manner. He tied the blood-vessels, or merely the veins of a portion of intestine, the

* Elements of Physiol. translated by Milligan, 4th ed. p. 314.

† Magendie, l. c. p. 358. ‡ Magendie's Journal de Physiol. ii. p. 117.

lymphatics being uninjured, and was then unable to kill a dog, even in an hour, by means of poison introduced into the intestine.

The results of Mayer's* experiments, in which he injected a solution of prussiate of potash into the lungs, must be more accurately detailed. As early as from two to five minutes after its injection into the lungs, the salt could be detected in the blood by the green or blue precipitate produced in the serum by the addition of muriate or sulphate of iron. The rapidity with which the prussiate of potash enters the blood is too great for it to be explained by means of the slow circulation of the lymph. The salt was detected in the blood long before it was perceptible in the chyle, and in the left side of the heart before a trace of it could be detected in the right cavities; while, if the absorption had been effected by the lymphatics, the course of the lymph being first into the venous blood of the body, the salt absorbed ought to be first detectible in the right cavities of the heart. Eight minutes after its injection into the lungs, prussiate of potash shows itself in the urine. It is found also in the skin, in the fluid of the articular cavities, in the abdominal cavity, in the pleura, in the pericardium, in the fat, in the fibrous membranes,—for instance, the dura mater,—in the aponeuroses, in the arachnoid, in the capsular and lateral ligaments, in the internal ligaments of joints,—for example, the cruciate ligaments of the knee-joints and the ligamentum teres of the acetabulum,—in the perichondrium, and in the valves of the heart.

The kidneys were the only glands in which it was detectible; prussiate of potash, like most salts, being excreted from the blood by the kidneys. The liver did not become stained on its external surface when the salt of iron was applied, but the colour was evident in the interior of the gland, although only around the large vessels which were inclosed in the cellular tissue of the capsule of Glisson; no change of colour was produced in the bile, and a very slight one only in the milk. In the testicle, salivary and pancreatic glands, and more especially in the cellular tissue of these parts, the colouring was more distinct. The spleen evidenced no change of colour, the suprarenal capsules scarcely any, and none was produced in the muscles except at the parts where the bundles of muscular fibre were enveloped in fibrous membrane. The nerves became green externally, but this was dependent on the cellular membrane which surrounded them; the nervous substance itself, and the brain and spinal cord, displayed not the slightest alteration of colour. The colour of the bone also remained unchanged. The reason of these differences is perhaps that the prussiate of potash is decomposed in some tissues so as to render its detection by chemical

* Meckel's Archiv. t. iii. 1817, p. 485.

tests impossible, for it must be distributed with the blood equally to all parts.

Some of the experiments which the Academy of Medicine of Philadelphia instituted,* seem to be opposed to the results of Mayer's experiments, and of all those hitherto mentioned. They seem to be in favour of the opinion of absorption being performed chiefly by the lymphatics. But they are not conclusive. The Academy found that after a solution of prussiate of potash had been injected into the peritoneum or intestine, the addition of a salt of iron thirty-five minutes or more afterwards to the chyle produced in the majority of cases a distinctly blue colour, while mostly a slight tinge was also produced in the serum of the blood and in the urine. The interval of thirty-five minutes is much too great; the blood and urine ought to have been examined, as in Mayer's experiment, a few minutes after the prussiate of potash was introduced. As these experiments were performed, they merely prove that chemical agents are absorbed by the lymphatics as well as by the capillaries. In one case (No. 36.) in which a cat was made to swallow one ounce of the solution of prussiate of potash, the experimenters found two minutes afterwards, when they let the animal bleed to death, that the salt could be detected in the urine, but not in the serum of the blood nor in the chyle; and nevertheless, the salt could have passed into the urine only through the medium of the blood. The commission of the Academy in several cases tied the vena portæ, and nevertheless nux vomica introduced into a portion of intestine produced tetanus in twenty-three or more minutes; while in other cases the mere ligature of the vena portæ produced death, but without tetanus. These experiments seem to prove that the lacteals had conveyed the poison into the blood, and it is possible for such to have been the case, in the space of twenty-three minutes; but this does not disprove the possibility of direct absorption into the blood in a shorter time. Moreover, branches of the portal veins of the intestines anastomose with those of the cava.† Westrumb‡ detected prussiate of potash in the urine two minutes after injecting it into the stomach, while the lymph and chyle contained none. The ureters had been divided, and tubes fixed in them, from which the urine was received.

Tiedemann and Gmelin have performed numerous experiments with colouring matter and salts which are easily recognised or detected by reagents. On examining the chyle several hours after colouring matters had been given by the mouth, they have never found it tinged, although the colouring substances were recognised in the blood and urine, and had already passed from the stomach into the intestine. In

* Philadelph. Journ. N. 6. Froriep's Not. N. 49.

† See page 185.

‡ Meckel's Archiv. vii. 525. 540.

very numerous experiments it was but a few times only that some portion of the salt taken into the stomach could be detected in the chyle: in a horse to which some sulphate of iron had been given it was detected afterwards in the chyle; and once in a dog which had taken prussiate of potash this salt was detectible in the chyle, but in a second experiment this was not the case; sulphocyanate of potash given to a dog was also once detected in the chyle. The objection, that the substances might be already all absorbed, is not tenable; for the intestine still contained a considerable quantity of them. These results, which, from the accuracy with which the experiments were performed, can be in great measure depended upon, agree with those of the experiments made by Halle* and Magendie.† On the other hand, they are opposed to those of Martin Lister and Musgrave,‡ of Hunter, Haller, and Blumenbach. Viridet and Mattei also assert that they have observed a yellow or red colour in the chyle after food consisting of yolk of eggs or red beet had been taken.

Fodera § filled a portion of intestine in a living animal with solution of prussiate of potash, tied it in two places, and then dipped it in a solution of sulphate of iron; the lacteals and veins became blue. Schroeder Van der Kolk, on repeating this experiment, perceived the blue colour in the lacteals only, not in the veins. After the lapse of half an hour, the solution of prussiate of potash in the intestine was not changed in colour, so that the sulphate of iron had not in that time permeated all the coats of the intestine. This does not absolutely disprove the immediate passage of substances into the blood; for the small quantities of the salt which would enter the blood are immediately carried onwards by the circulation, while the motion of the chyle in the lacteals being proportionally slow, foreign matters absorbed with it would be more exposed to the test. Besides, a blue tint is exceedingly difficult to detect in the blood itself, and cannot be recognised with certainty except in the serum of the blood. Lawrence and Coates || did not detect the salt in the blood before it was perceptible in the upper part of the thoracic duct.

Several experiments to determine the influence of ligature of the thoracic duct on absorption have been made by Brodie, Magendie, Delille, and Segalas. In Brodie's¶ experiments, the fatal effects of alcohol and Worara poison were still produced, after the thoracic duct was tied.

Since, however, the thoracic duct has sometimes in animals communications with veins,—for instance, branches joining the vena azygos, as in the hog,—and since even a right thoracic duct sometimes exists, while the absorbent vessels have frequent communications with each other, the application of a ligature to the thoracic duct cannot absolutely prevent the passage of the poisoned lymph into the blood.

* Fourcroy's Système des Connaiss. Chim. 10. 66. † Loc. cit.

‡ Phil. Trans. 1701. 819.

§ Recherch. exp. sur l'exhalation et l'absorption. Par. 1824.

|| Froriep's Not. 77. ¶ Phil. Trans. 1811.

Emmert has demonstrated the immediate passage of matters into the blood, by showing that they do not enter the circulation when the blood-vessels are tied. Emmert* tied the abdominal aorta, and then introduced prussiate of potash and a decoction of angustura virosa into different wounds in the feet. The prussiate of potash was absorbed and detected in the urine, but the angustura had not its usual poisonous effects. In another experiment, in which Emmert, after tying the abdominal aorta, introduced prussic acid into a wound of the foot, no effects had ensued even in seventy hours; but, on loosening the ligature on the aorta at the end of that time, the symptoms appeared in half an hour. Jacobson,† lastly, has shown, that in mollusca, which possess no lymphatics, prussiate of potash, nevertheless, finds its way readily into the blood from every surface to which it is applied, and is again eliminated from the blood by the secreting organs,—the lungs, liver, and saccus calcareus.‡

The immediate absorption of matters by the capillary blood-vessels is proved by all these experiments, but especially by the extraordinarily rapid effects of poison; for it is equally certain that the general effects of poisoning depend, not on nervous communication, but wholly on the noxious substance entering the circulation.

All the phenomena which we have detailed might, however, be dependent on absorption by the lymphatics, if, as some recent writers suppose, the lymphatics and small veins do really communicate.§ But this objection may be completely set aside by the known laws of the imbibition of animal tissues.

Imbibition.—Hitherto the passage of matters into the blood has been supposed to depend on a peculiar absorbing power of the veins. But it can be shown that fluid matters find their way without the aid of this imaginary power of absorption into the blood of the capillaries; and from the capillaries they necessarily pass first into the veins, the direction in which all the blood of the capillaries moves being from the arteries towards the veins and the heart. The primary phenomenon of the immediate absorption of substances in solution into the blood is the permeation of the animal tissues by the fluids. The property of permea-

* Meckel's Archiv. i. 1815, p. 178. Schnell, Diss. sist. hist. veneni upas antiar. Tub. 1815. Tübing. Blätter. 3. 1. 1817.

† Froriep's Notiz. xiv. p. 200.

‡ On the subject of absorption by the capillaries and veins, consult Westrumb, Physiolog. Untersuch. über die Einsangkraft der Venen. Hannover, 1825. Tiedemann und Gmelin, Versuche über die Wege, auf welchen Substanzen aus dem Magen und Darmkanal ins Blut gelangen. Heidelb. 1820. Seiler und Ficinus in Zeitschrift für Natur- und Heilkunde, ii. 378. Jaeckel, De absorptione venosâ. Vratislar, 1819. Lebkuckner, Diss. utrum per viventium adhuc animal. membran. atq. vasor. parietes mater. ponderab. illis applicat. permeare queant, nec ne. Tüb. 1819. Wedemeyer, über den Kreislauf. Hannover, 1828. 421. Schabel, de effect. veneni rad. veratri albi et hellebori nigri. Tub. 1819.

§ See p. 272.

bility by fluids possessed by tissues even after death, depends upon their invisible porosity, and is termed imbibition. This kind of absorption being exercised by animal textures wholly devoid of life, may be correctly termed the inorganic, in contradistinction to the lymphatic absorption.

Gases, and thin fluids, together with the matters they hold in solution, permeate moist animal textures. Two kinds of gases in contact with the two surfaces of a moist animal bladder, one being within it and the other external to it, each permeate the bladder till they are equally mixed. The bladder having been previously dried and then moistened does not prevent this process taking place. A gas will permeate a moist bladder, to be absorbed by a fluid within it. This explains how it is that gaseous matters can enter into the blood during respiration, without the globules of the blood escaping. The gaseous matters permeate the membranes of the lungs, and are dissolved in the blood circulating in the numerous capillaries which traverse these membranes, by virtue of the invisible porosity of the coats of the vessels, which, nevertheless, have no openings large enough to admit the red particles of the blood. If a piece of moist bladder is tied over a bottle completely filled with water, so that the bladder is in contact with the surface of the water, and if some salt is then strewed over the outer surface of the bladder, the salt is dissolved by the water which permeates the pores of the bladder, and from this water is imparted to the water in the vessel. The primary cause of imbibition, or the permeability of animal tissues, is therefore the tendency which substances have to diffuse themselves uniformly in the fluid in which they are dissolved. A salt in solution has a tendency to diffuse itself through any other fluid with which it is miscible. Salt water and water, for example, when in contact, become uniformly mixed with each other. Animal tissues owe their softness to the watery fluids which they contain, and which fill their pores. Any matter in solution, therefore, which comes in contact with them will tend to diffuse itself in the fluids of the pores, and again, through the medium of these pores, with fluids in contact with the opposite side of the membrane, until the distribution of the matters dissolved is uniform in the two fluids which the membrane separates. There are, however, particular circumstances in which the process of imbibition is accelerated by attraction, and by the action of capillary tubes. The latter is the case when a dry animal texture is moistened, in which case the capillary attraction of the empty pores must favour the entrance of the fluid. The first case is displayed in the phenomenon of endosmose and exosmose, first discovered by Parrot, and farther investigated by Porret, Dutrochet, and others. If a solution of any salt, or of sugar, is poured into a glass tube closed below by a piece of bladder, the particles of the solution permeate the pores of the bladder, but do not pass through it. If the tube thus filled is placed

in a vessel containing distilled water, the fluid gradually rises, and sometimes to the extent of several inches, within the tube, and by proper tests it is found that at the same time a portion of the solution has found its way from the interior of the tube to the water external to it. The elevation of the level of the fluid in the tube continues till the two fluids are homogeneous. If the tube contains water, and the exterior vessel the saline solution, the water sinks in the tube. If both vessels contain solutions of different salts, but of the same density, the level of the fluids does not alter, but the two salts become equally mixed. If, on the contrary, one solution is more concentrated than the other, the quantity of the more concentrated one becomes increased. The same phenomena are observed when, in place of the bladder of an animal, porous mineral substances are used. Two explanations of the phenomena have been given. The first, which was offered by Magnus and Poisson, is, that between the particles of a saline solution a compound attraction is in play, consisting of the mutual attraction of the salt and the water for each other, of the attraction between the individual particles of the water, and of that between the individual particles of the salt. This compound attraction is supposed to be more powerful than the simple attraction between the particles of water solely.* The second explanation is the following: the animal bladder, inasmuch as it is porous, may be viewed as a system of capillary tubes which exercise an attraction on the fluids, which have a tendency to mix with each other, through the medium of the water which fills the pores. If, now, it be imagined that one of the fluids is more strongly attracted by the tissues of the bladder than the other, it will, of course, be longer retained in its passage through the pores; and the level of the fluid which passes through most quickly will necessarily fall in the vessel that contains it, while the level of the former will rise until the increasing pressure of the rising column of water counterbalances the effect of the more powerful attraction.†

Dutrochet has named the phenomena which we have described "endosmose" and "exosmose," according as the quantity of the one or of the other fluid increases under different conditions. In the direct passage of matters in solution into the capillaries and the blood, endosmose without doubt takes place, and not merely simple imbibition. Dutrochet has demonstrated this by experiment. A portion of the intestine of a young fowl, half filled with a solution of gum, sugar, or common salt, and tied at both ends, was placed in a shallow vessel filled with water, when it soon became filled to distension. If, on the contrary, the intestine contained pure water, and was immersed in sugared water, it became gra-

* Berzelius, loc. cit. p. 134.

† Biot, Experimental-Physik, translated into the German by Fechner, i. p. 384. See also Poisson, in Poggendorf's Annal. xi. 134. Fischer, ibid. 126. Magnus, ibid. x. 153; and Wach, Schweigg. Journal, p. 20.

dually more lax, and the fluid in the intestine was afterwards found to contain sugar.*

Dutrochet's hypothesis, that electric action is connected with these phenomena, has not been confirmed. It does not also constantly happen that the denser fluid attracts more of the thinner than the latter does of the former: in the case of gases especially, the contrary is seen to be sometimes the case. But the chemical constitution of the fluid, and its physical and chemical relation to the animal membrane which it permeates, seem to have an important influence on the phenomenon. Dilute alcohol kept in bladder becomes more concentrated, the water alone evaporating;† and it has been found that if a portion of the intestine of a fowl filled with a watery solution of acacia gum and rhabarbarin, and tied close, is laid in a vessel containing water, the intestine becomes distended, while the rhabarbarin exudes from it. Similar sacks filled with a weak solution of sulphate of iron, and laid in solution of ferrocyanate of potash, became distended in consequence of the endosmosis of the water of the exterior solution, which at the same time acquired a blue colour from the salt of iron having passed through the membranes in an outward direction, while the absence of this colour in the fluid in the interior of the portions of gut proved that the salt of potash had not permeated them. The phenomenon of the endosmosis of gases, on which M. Faust‡ has instituted experiments, are very remarkable. A bladder half filled with atmospheric air being placed under a jar containing carbonic acid becomes more distended; and if the bladder which is placed in the carbonic acid gas contained hydrogen, it becomes distended to bursting. If, on the contrary, the jar contains the lighter, and the bladder the denser gas, the bladder becomes collapsed.

Time required for absorption by the capillaries.—I wished to know the time required for any substance to reach by the way of imbibition the superficial layers of the capillaries of a part which is not invested by epidermis, so as to enter the circulation. The delicate membrane which forms the villi of the intestines in the calf and ox contains capillary blood-vessels, although the villi themselves measure only $\frac{1}{530}$th of an inch in diameter. From this measurement we can conceive to what depth fluids must permeate to reach the capillaries of any membrane free from epidermis. Having put into a glass vessel with a very narrow neck some solution of prussiate of potash, I tied over it in one experiment the urinary bladder of a frog, in another the lung of the same animal, then with a hair-pencil applied to the surface of the soft membrane some solution

* Dutrochet, L'agent immédiat du mouvement vital. Paris, 1826. Nouv. Rech. sur l'endosmose. Paris, 1828. [See also the article Endosmose in the Cyclopædia of Anatomy.]

† See experiments of Staples in Kastner's Arch. für Chemie, Bd. iii. H. 1—3. p. 282.

‡ Amer. Med. Journ. vol. vii. Froriep's Not. N. 646.

of a salt of iron (the muriate), and at the same moment inverted the glass, so that the solution of prussiate of potash came in contact with the inner surface of the membrane. A second of time had not elapsed when a pale blue spot formed, and soon became more distinct. It appears, therefore, that substances in solution permeate a membrane of the thickness of the stretched bladder of a frog in detectible quantity within a second of time. The membrane forming the frog's bladder consists of several layers, and is very much thicker than the organised membrane which forms the intestinal villi. We may therefore safely admit, that substances in solution permeate in detectible quantity a membrane not covered by epidermis, so as to reach the first layer of capillaries, and thus to enter the circulation in a shorter time than a second. Now the blood, according to Hering's calculation, circulates through the whole body in half a minute, and, according to others, in from one to two minutes; consequently we may suppose that a detectible quantity of any substance in solution, which comes in contact with a membrane free from epidermis, may be distributed through the circulating system in from half a minute to two minutes.

Action of poisons.—The narcotic poisons act, it is true, by abolishing the nervous energy, but, when applied locally to the nerves, their effects are only local. I held the nerve of a frog's leg, which was separated from the body, in a watery solution of opium for a short time, and that portion of the nerve lost its irritability, *i. e.* its property of exciting twitchings of the leg when it was irritated; but below the part that the poison had touched the nerve still retained this function. Opium, therefore, produces a change in the nervous matter itself; but the influence is local, and is not propagated through the nerves, so as to produce general poisoning. Frogs are very sensible to the effects of opium; and nevertheless, if the leg of a frog is separated from the body, the nerve only being left to maintain the connection, and is then placed in a solution of opium, and kept there for several hours, the animal suffers no narcotic influence; provided, however, that it is so confined, that in its struggles it cannot throw any of the fluid over its body.

These experiments, as well as many others, instituted by well-known physiologists, prove that, before narcotic poisons can exert their general effects on the nervous system, they must enter the circulation. Dupuy and Brachet indeed maintain that animals cannot be destroyed by narcotic poisons introduced into the stomach, if the nervus vagus has been divided on both sides, or, at least, that they do not die so soon. But in thirty experiments on mammalia, which M. Wernscheidt performed under my direction, not the least difference could be perceived in the action of narcotic poisons introduced into the stomach, whether the nervus vagus had been divided on both sides or not, provided the animals were of the same species and size.

The rapid action of the greater number of narcotic poisons is perfectly explicable by the facts above detailed respecting absorption by imbibition. Prussic acid, however, exerts its influence in a much shorter time than would be required for it to enter the circulation through the medium of the capillaries, which, as we have said, is half a minute, or two minutes. The spirituous solution of extract of nux vomica, also, introduced in small quantity into the mouth of a young rabbit, produces immediate death; whereas when applied to a nerve at some distance from the brain,—for instance, to the ischiadic nerve,—it produces no general symptoms. Concentrated prussic acid, also, as Wedemeyer observed, does not exert its poisonous influence when applied merely to a bare nerve. The rapid effects of prussic acid can only be explained by its possessing great volatility and power of expansion, by which it is enabled to diffuse itself through the blood more rapidly than that fluid circulates, to permeate the animal tissues very quickly, and in a manner independent of its distribution by means of the blood, and thus to produce the peculiar material changes in the central organ of the nervous system more quickly in proportion as it is applied nearer to it.

Passage of ingesta into the secretions.—The rapidity with which fluid matters are imbibed into the capillaries, and distributed through the body by the circulation, explains completely the quick reappearance in the urine of substances which have been taken into the stomach with the food, without the need of having recourse to the barbarous notion of secret passages existing between the stomach and kidneys. According to Westrumb, soluble salts find their way into the urine in from two to ten minutes after they are taken into the stomach; for, when this time had elapsed after giving prussiate of potash to an animal, he was able to detect it in the urine which he collected immediately from the ureter. Stehberger's experiments, however, prove that the reappearance in the urine of substances taken with the food ordinarily requires a much longer period.

Absorption of chyle.—The matters which pass by imbibition through the walls of the capillaries into the blood must, however, be in solution; they must not consist of globules. This condition alone shows that the digested matters, and the chyle which contains globules, cannot find their way by imbibition into the capillaries and the venous blood. Tiedemann, Gmelin, and Mayer, have, it is true, observed streaks of chyle in the intestinal and portal veins. But the chyle could not have entered the blood through the walls of the capillary vessels; for, if that were the case, the corpuscules of the blood in the capillaries would likewise be able to escape from them. Perhaps the streaks of chyle observed by these physiologists were derived from the communications which are supposed, although not yet proved, to exist between the lacteals and the small veins.

Endosmosis, however, *does not explain the absorption of all fluids* by the animal tissues. If the fluids of the tissue itself are more concentrated than those to be absorbed, such as fluids collected in the pleura, or lungs, the passage of the external fluids into the parenchyma will, according to the laws of endosmosis, take place more readily than the passage of the fluids of the tissue outwards. But if, on the contrary, the external fluid is equally concentrated with that contained in the tissue, the two fluids ought, according to the laws of imbibition, to pass through the membrane in both directions with equal rapidity, so that the quantity of both fluids would remain the same; and, if the fluid of the tissue is the less concentrated of the two, it will exude in greater quantity than the external fluid will be absorbed, so that the quantity of the latter will be increased. Imbibition, therefore, does not explain the diminution of the quantity of fluids by absorption, but only the mingling of them, as in the case of poisons applied to the surface of the body, &c. For a collection of fluid in the pleura, containing albumen and salts in the same state of concentration as these substances exist in the blood, would not be diminished in quantity by imbibition alone; there would be merely an interchange of the saline matters contained in the external fluid and in the blood, while the bulk of the former would remain the same; and, if the saline ingredients were in a more concentrated state in it than in the blood, its quantity would even become increased.

The removal of collections of fluids by absorption must be effected in many cases either by means of the lymphatics, independently of imbibition into the capillaries, or we must suppose that the suction of the venous blood towards the heart assists the absorption by the capillaries. It is possible that the process of endosmosis may be modified by a peculiar attraction exerted by the tissues on the fluids circulating in them; an attraction, by the agency of which the fluids in the tissues may be retained while the external fluid is absorbed, so that merely absorption, and not an interchange of fluids, as is the case under ordinary circumstances, is the result. Water, for example, would have a tendency to diffuse itself in the blood of the capillaries; but the blood being under the influence of the mutual vital process which is going on between it and the capillary vessels, would have no tendency to diffuse itself in the water. The red particles of the blood have, as we have already seen,* a great affinity for water, and in their passage through the capillary vessels they may contribute to cause its absorption.

Absorption by organic attraction.—The question whether the blood in the capillary vessels, or these vessels themselves, exert on certain substances an attraction which differs in its nature from any accounted for by physical laws, is quite distinct from the one above discussed. There

* See page 105.

is only one part of the body in which this kind of attraction certainly exists, and that is the capillary system of the placenta. The existence of lymphatics in the placenta and umbilical cord being quite problematical, the transmission of nutritive fluids from the mother to the child must be effected by means of the capillary vessels of the placenta. There is no direct communication between the vessels of the mother and those of the fœtus, the sole mode in which the uterine arteries terminate is by becoming continuous with the radicle uterine veins; and, on the other hand, the fœtal arteries of the placenta have no other mode of termination than in the commencing fœtal veins of the same part. Weber* has given a very interesting description of the mode in which the placenta and uterus are connected. The finest ramifications of the placental vessels are distributed in the tufted processes on the maternal surface of the placenta. The arteries ramify in the tufted villi, and terminate at the extremities of the villi by direct inosculation with the radicles of the placental veins. Bundles of these tufts of villi project into the cavities of the large veins, in which the maternal blood flows on the inner surface of the uterus. From this arrangement of the tufts, and from the delicacy of the coats of the uterine veins, the fœtal blood circulating through the capillaries of the placental tufts is freely exposed to the action of the venous blood of the mother, and probably attracts from it some of the matters dissolved in it.

In the endosmosis which undoubtedly takes place between the fœtal and maternal blood, more matter is received by the fœtal blood than is given in exchange by it to the blood of the mother. It is an organic and vital endosmosis totally different in the laws which regulate it from the chemical process of imbibition described by Dutrochet. In ruminating animals the tufts or villi of the cotyledons of the ovum are not imbedded in the veins of the uterus, but, like roots in the ground, in sheath-like cavities, or tubes, hollowed in the substance of the uterus. All these excavations in the uterus are lined with capillaries of the maternal vessels; while the capillaries of the fœtus, which have no communication with those of the mother, are distributed upon the tufts of the cotyledons. Here the matters which are to be absorbed by the capillaries of the fœtus must first be secreted by those of the mother.

Does the action of the heart aid absorption?—It is still matter of doubt whether the absorption of fluids into the capillaries by means of imbibition is aided by the motion communicated to the blood in the veins, and thence to that in the capillaries, by the sucking action which the heart exerts in the dilatation of its cavities. The motion of the blood, however, must be so far favourable to imbibition, as it removes what has already been absorbed, and thus renders constant the cause of the endosmosis,—namely, the tendency of substances to diffuse themselves

* Hildebrandt's Anatomie, Bd. iv. p. 496.

through fluids till equally distributed. If the same portion of blood were constantly exposed to this action, imbibition would after a time necessarily cease.

Influence of galvanism on imbibition.—Fodera* has observed that absorption, or imbibition, is accelerated by the action of galvanism. He injected prussiate of potash into the pleura, and sulphate of iron into the abdomen. Usually five or six minutes elapse before these two substances combine; but their combination was instantaneous when a slight galvanic current was passed through the diaphragm. The same phenomenon is said to occur when one fluid is introduced into the urinary bladder, the other into the abdomen, or one into the lung, the other into the pleura. The nerves have no influence on inorganic imbibition; there was, in my experiments, no perceptible difference in the absorption of poisons whether the nervus vagus had been divided or not.

Changes produced in the matters absorbed.—Matters which find their way from the intestines into the circulation by permeating the coats of the capillaries, do not pass directly from the intestinal veins into the vena cava, they circulate through the liver before reaching the general circulation. Magendie has observed, that in their transit through the liver the properties of many substances are altered. Thus, if a gramme† of bile, or a considerable quantity of atmospheric air, are injected into the crural vein, immediate death is the consequence; while, if they are injected into the vena portæ, the animal suffers no ill effect. Many substances undergo a change in the intestines themselves. Thus the poison of the viper, when taken into the stomach, produces, according to Redi and Mangili,‡ and Dr. Stevens,§ no poisonous effects; and the saliva of hydrophobia, according to Coindet,|| does not exercise its infectious property when taken into the alimentary canal.

Effect of plethora on absorption.—Magendie has observed that distension of the blood-vessels, with an excess of fluid, diminishes the activity of absorption. By the injection of water into the veins, the absorption of foreign substances by the organised membranes was prevented; but, after taking some blood from the animal, absorption commenced with the usual phenomena. Venesection, on the contrary, accelerated the process; so that phenomena, which ordinarily did not ensue till after two minutes, appeared in half a minute. Absorption is most rapid from the mucous membranes, from serous membranes, and from wounds; it is much slower from a membrane covered with epidermis.

Absorption by the skin.—The most external layer of the organised cutis seems indeed to possess a very feeble absorbent power: this may perhaps arise from its secreting horny matter. Colouring matter, consisting of granules or grains of powder from an explosion, having found

* Journ. de Physiol. iii. p. 35.

† About 15½ grains avoirdupois.

‡ Meckel's Archiv. iii. 1817, p. 639.

§ On the Blood, p. 137.

|| Froriep's Notiz. 1823, Sept. 170.

their way into cracks of the skin, remain during the entire life without being dissolved or absorbed. Nitrate of silver given internally for a considerable time, imparts a blackish slate-colour to the skin, probably from a chemical combination being formed between the silver and the animal matter. The skin covered with epidermis, however, is certainly endued with an absorbing power; but the substances to be absorbed must be either in solution, or readily soluble in the animal fluids. The subject of absorption by the skin is important, on account both of the frequency with which foreign substances come in contact with it, and from its being adapted to the application of medicinal substances. Seiler and Ficinus found that when the feet of horses had been moistened with solution of oxide of lead in liquor potassæ, this substance was detectible in the blood and chyle.*

All metallic preparations rubbed into the skin have the same action as when given internally, only in a less degree. Mercury applied in this manner cures syphilis, and excites salivation; tartrate of antimony, according to Letsom and Brera, excites vomiting; and arsenic exerts its poisonous effects. Vegetable matters also, if soluble, or already in solution, exert their peculiar effects through the medium of the skin. Haller states that white hellebore laid upon the abdomen excites vomiting, and that violent purging is produced by washing the feet with a decoction of either the white or the black hellebore. Sabadilla seeds applied to the skin were found by Lentin to excite most violent cramps, and when rubbed on the abdomen to cause purging. Cantharides applied to the skin excite strangury; and narcotics thus applied produce their peculiar effects. Camphor, Magendie says, can be detected in the vapour expired from the lungs; oil of turpentine by the violet smell of the urine; mercury in the blood, saliva, urine, and milk, according to Bloch, Autenrieth and Zeller, and Canter, and in the bones also, according to Fricke;† prussiate of potash, rhubarb, and madder, in the blood, urine, &c.; each of these substances having in the respective cases been applied to the skin. But the action of all medicinal substances and poisons applied to the skin is much more powerful if the cuticle has been previously removed.

It has long been a contested question whether the skin covered with its epidermis has the power of absorbing water, and it is a point difficult to determine, because the skin loses water by evaporation.

The epidermis is certainly hygroscopic, and swells when placed in water. The experiments of Falconer, Alexander, and others, which consisted in weighing the body and the water in baths, appear to me unworthy of dependence. Seguin‡ and Currie§ could discover no in-

* On this subject consult Westrumb, Meckel's Archiv. 1827; and Sewall, ibid. ii. 146.

† Horn's Archiv. 1826. 459.

‡ Ann. de Chimie, t. xc. 185; t. xcii. 33. Meckel's Archiv. iii. p. 385.

§ Med. Reports, ch. xix,

crease of weight when the whole or part of the body was immersed in water; and those experiments in which colouring matter or prussiate of potash dissolved in the water of a bath could afterwards be detected in the urine, by no means prove that the water was absorbed. Saline substances can permeate a membrane both sides of which are in contact with water, without the level of the water on either side undergoing any change.

[M. Edwards* has proved most clearly that this absorption of water by the surface of the body takes place in the lower animals very rapidly under certain circumstances. Not only frogs, which have a thin skin, but lizards, in which the cuticle is so very much thicker than in man, after having lost a great part of their weight by being kept for some time in a dry atmosphere, were found to recover both their weight and plumpness very rapidly when immersed in water. Merely the tail, posterior extremities, and posterior part of the body of the lizard were immersed, but the water absorbed was distributed throughout the system. M. Edwards thinks it impossible not to attribute this property to the skin of man, if the scaly skin of the lizard possesses it. The result of Seguin's experiments, namely, that there was a loss of weight during the immersion in water which was equal to the loss by pulmonary perspiration under other circumstances, is explained by M. Edwards, by supposing that the absorption and transudation by the skin were equal, so as to balance each other. M. Seguin supposed that neither took place. Two causes are found to exert a great influence over these two functions of the skin in the lower animals: 1st, the quantity of fluid already in the body; and, 2ndly, the temperature of the water in which it is immersed. Fulness of body renders absorption less, and lowness of temperature diminishes the exudation. To render absorption by the human skin perceptible, the exudation must not only be depressed below the amount of the absorption by the skin, but the absorption must be so great as to balance the loss by pulmonary exhalation. This can seldom happen. M. Edwards finds also that there is a perceptible absorption by the skin of the lizard in humid air; and in an experiment made on several Guinea pigs kept in a moist atmosphere, he found that the average weight of their evacuations exceeded the loss in the weight of the animals. On comparing this result with the loss of weight of Guinea pigs kept in a dry air, he was inclined to attribute the excess of weight of the evacuations to the absorption of watery vapour. But it is even more difficult, M. Edwards observes, to prove the absorption by the skin in a moist atmosphere than in water, and it must be much less abundant, more particularly in warm-blooded animals; for, their temperature being generally higher than that of the surrounding air, the air becomes rarefied around them, and thus more susceptible of imbibing moisture.]

* On the influence of physical agents on life, pp. 181. 189.

The absorption of different kinds of gas by animal tissues, as in the process of respiration, and even by the skin itself, is placed beyond doubt by the experiments of Abernethy, Cruikshank, Autenrieth, Beddoes, and Collard de Martigny. In these cases, of course, the absorbed gases combine with the fluids, and lose the gaseous form. Several physiologists have observed an absorption of nitrogen by the skin: Beddoes says that he saw the arm of a negro become pale for a short time when immersed in chlorine; and Abernethy observed that when he held his hands in oxygen, nitrogen, carbonic acid, and other gases contained in jars over mercury, the volume of the gases became considerably diminished.

Interstitial absorption.—It is still a matter of doubt whether the absorption which goes on in the substance of the different textures of the body is chiefly performed by the blood-vessels, or by the lymphatics. In many parts, however, in which the existence of lymphatics has never been demonstrated,—for example, in the bones,—there is marked evidence of absorption going on.

In many other cases in which matters are absorbed from parts known to possess lymphatics as well as blood-vessels, it is quite uncertain into which order of vessels these matters are first received. This is the case in the following instances: the reabsorption of the colouring matter of the bile deposited in the different tissues in jaundice, and the absorption of accumulated secretions, such as bile and urine, into the circulation; the wasting of the thymus gland during the period from infancy to the twelfth year; the disappearance of the fat from the body generally in persons fasting, in consumptive persons, after great losses of the fluids of the body, and in animals during hybernation; and the frequently rapid disappearance of warts from the fingers. These cases of absorption are not all of the same kind. The true interstitial absorption of organised tissues, in which the particles of the tissue which fill the meshes of the capillary network are removed, must be distinguished from the cases of the absorption of fluids, which do not form part of the tissue, and have therefore no mutual vital action with the blood-vessels. In the process of interstitial absorption, as it occurs in the atrophy of the tail of the tadpole, and of the pupillary membrane in the fœtus, and in the developement of cells in the bones, the most essential circumstance, perhaps, seems to be the solution of the particles which occupy the meshes of the capillary system. The matter when dissolved may be removed by imbibition into the currents of blood, or, except in the case of the bones, by absorption by the lymphatics. Of all organised parts, the bones present the phenomena of interstitial absorption in the most remarkable degree; their cells are developed in the child long after the bone is formed, and increase in size by the agency of the same process. The diploe of the cranial bones disappears in old age, and the bones become thinner. The frontal and sphenoidal sinuses are deve-

loped in the period of youth. Parts, however, which are not organised, but are only in connection with an organised matrix,—for example, the roots of the teeth,—are also subject to absorption. The roots of the first teeth disappear at the time of the change of the teeth; and Soemmering* has observed that they become soft, probably in consequence of solution of their component matter. In caries, also, which depends on an abnormal combination of their components, the teeth are acted on by the fluid of the mouth and softened. It is still unknown whether necrotic portions of bone which remain long in contact with living textures, diminish in size.

When, in consequence of diseased states of the blood, of paralysis, or other causes, nutrition is less active, the interstitial absorption is no longer counterbalanced, and the part wastes. Whether in phthisis the muscular fibres themselves waste, or merely the cellular membrane in their interstices, is uncertain. Their muscles, however, such as the platysma myoides, and some muscles of the external ear, seem really to waste. In paralysis the wasting of the muscles is more frequent; and Schroeder Van der Kolk has even observed their conversion into fat. Cartilage, bone, brain, and nerves, according to Desmoulins' and Schroeder's researches, do not waste in phthisis. When the cause of atrophy is general, the tissues are absorbed in the following order: fat, cellular tissue, muscles, bone, cartilage, and tendon. Long-continued pressure, by putting a stop to nutrition, may cause every tissue to be absorbed. The mode in which pressure acts in causing the absorption of bone, is, however, a problem still requiring solution; for if the cessation of nutrition in consequence of the pressure were the sole cause, the articular heads of the bones of the lower extremities ought also to be absorbed. Perhaps a swelling affecting all surrounding parts—an aneurysm, or fungus,—excites inflammation of the bone, as well as of other parts; and bone when inflamed becomes softened, and is consequently more readily susceptible of absorption when its nutrition happens to be interrupted by any pressure. Caries, however, is not produced in these cases.† It is a well-known fact that iodine favours the wasting and absorption of organised tissues.

b. *Of exhalation and exudation.*

Many matters dissolved in the animal fluids, particularly foreign substances which have been taken up into the circulation, and which are then distributed through the body with the blood in their original state, or more or less altered, are afterwards eliminated from the system by the process of imbibition and endosmosis. Prussiate of potash, having

* Vom Bau des Menschlichen Körpers, i. § 226 u. 233.

† On this subject consult Schroeder V. d. Kolk in Luchtmann, De absorptionis sanæ et morbosæ discrimine. Traj. ad R. 1829.

entered the circulation by endosmose, permeates the tissues which form the surfaces communicating with the exterior, according to the same laws, and becomes mingled with the natural secretions. In this way it soon appears again in detectible quantity in the most various secreted fluids; in the urine, for instance, it may be detected, according to Westrumb, in from two to ten minutes after its introduction into the body. The blood impregnated with prussiate of potash, and the fluid contained in the cavities of a secreting organ,—for example, the urine in the tubuli uriniferi of the kidney,—are able, in accordance with laws purely physical, to impart to each other the substances that they contain in solution until these substances are equally diffused in both. In jaundice almost all the internal organs, as well as the secretions, become impregnated with the colouring matter of the bile, which is contained in the serum of the blood.

Those natural or accidental ingredients of the blood which are capable of assuming the gaseous form may, unless they are retained by some special attraction exerted on them by the tissues, evaporate from the free surfaces of the membranes of the body.

When pressure favours their passage through the pores of the animal membranes, even fluids must, in accordance with physical laws, force their way into the free cavities filled with gas or vapour;—hence the effusion of fluids in the animal body after death as the effect of mere gravitation; serum, at first pure, afterwards with the colouring matter of blood dissolved in it, permeates the tissues, and may collect in the different cavities; the bile exudes from the gall-bladder, and colours yellow the parts which are in contact with it. During life, absorption effected by an attraction of a vital nature counterbalances this transudation of fluid through the membranes of the body; but in disease different causes destroy the balance of the two processes, and then the water, with the animal matter and salts dissolved in it, collects in the cavities of the body and in the cellular membrane, and gives rise to the appearances of anasarca or œdema, and albuminous urine. Obliteration of the great venous trunks of the viscera or of the extremities gives rise to exudation of albuminous fluid into the surrounding serous sacs or into the cellular membrane, particularly of the inferior extremities; and artificial dropsy of the cellular membrane may be produced, as Bouillaud has shown, by tying the great venous trunks. The dropsies occurring in consequence of degeneration of the viscera may possibly be also partly dependent on the circulation through the viscera being obstructed. The exudation of the fibrinous fluid in inflammation might be explained in the same way; but the quality of the exuded matter depends on other causes.

Exudation during life.—The foregoing observations would seem to show that the exhalation of vapour, and exudation of fluid, are, even in

the living body, the result of the purely physical laws of imbibition, endosmosis, and pressure. But that is not the case. If exudation during life was solely under the influence of these physical laws, all the ingredients of the fluids would escape equally; but the matter which permeates the tissues, and is exhaled or exuded, often consists of a part only of the substances which are contained in solution in the blood. Thus in inflammation the matter which exudes through the membranes is the fibrin which the serum of the blood holds in solution; while, on the contrary, in dropsies,—such as are produced, for example, by obstruction to the return of venous blood,—the fibrin does not exude; the exudation is merely an albuminous fluid. There must, then, under ordinary circumstances, be some force in action which prevents the escape of fibrin from the vessels, and which in inflammation is rendered inert,—some affinity or attraction which the parenchyma possesses for the fibrin, but not for the albuminous serum, which therefore in anasarca is allowed to escape. At the commencement of inflammation, as observed in a wound, or after the application of a blister, serum merely is effused; when the inflammation becomes more violent, the fibrinous part of the blood also exudes.

It is most probable that there are similar differences in the exhalation of fluids in the gaseous form, for instance, from the skin; and that not every part of the fluids of the body which is capable of assuming the form of vapour, is really exhaled from the surface of the membranes.

Secretion.—The elimination of many substances from the blood cannot be explained according to the laws of endosmosis. The urea, for example, which has been proved to exist already formed in the blood itself,* is nevertheless excreted by no other part of the body than the kidneys.

Other excretions, formed of components of the blood, are formed only under certain local conditions. This is the case with the menstrual flux, which, according to the observations of Lavagna, Toulmouche, Brande, and myself, contains no fibrin; the clots which form in it are soft, and consist principally of red particles alone. Brande is certainly wrong in saying that the menstrual fluid is merely a concentrated solution of the red colouring matter of the blood; I have found red particles in it perfectly unchanged in appearance. It must therefore be supposed that, at the period of menstruation, the texture of the vessels of the uterus becomes so loose as to allow the escape of the red particles. There are no open mouths of veins in the uterus any more than in other parts of the body.

In the cases also in which the blood itself escapes slowly from the surface of membranes, by what is called exhalation, secretion, or "diapedesis," there is more than a simple secretion or transudation; the coats of the vessels must be changed in texture, and in many cases,—as for ex-

* See page 151.

ample in hæmoptysis and in the bloody expectoration which accompanies inflammation of the lungs,—if not in all, there is rupture of the minute vessels or capillaries. The observations of Wedemeyer,* however, render it probable that, under particular circumstances, the colouring matter of the red particles may, even in living animals, be dissolved in the serum, and thus give rise to a coloured effusion. Having injected a considerable quantity of warm water into the veins of horses, he found that exudation of serum, of a red colour, took place from the nostrils, and into the abdominal cavity. The colouring matter of the red particles is, it is known, soluble in water; and in scurvy, purpura, and after the bite of poisonous snakes,† it seems to be dissolved in the serum. A certain talented physician supposes the exhalation of blood or "diapedesis," of which we have spoken above, to be a mere exudation of a solution of colouring matter without any entire red particles. This is a difficult matter to prove, and until proved cannot be admitted as a fact. Even the bloody appearance of the serum of the blood in scurvy may arise, not from cruorine being dissolved in it, but from its containing a few red particles diffused through it, which is very likely to happen when blood does not coagulate firmly.

The globules of secreted fluids must be supposed to be formed at the moment that the secretions are separated from the blood; they could not have passed entire through the coats of the vessels. The globules of pus, for instance, which are larger than the red particles of the blood, and in part, according to Weber, twice as large, cannot be those bodies merely changed in some way. They must either be particles of the tissue separated from the suppurating surface, or they must be formed at the very moment of the elimination of the secretion, as the observation of Brugmans and Autenrieth, that pus, when first formed, is a thin and clear fluid, would seem to indicate. The elimination, by the kidneys, of globules of pus which had found their way into the blood, is quite an impossibility; the proximate components only of the pus in a state of solution can be eliminated from the blood, the globules must be formed from these components afterwards.

* Ueber den Kreislauf; Hanover, 1828; 463.
† Autenrieth, Physiol. ii. 154.

SECTION III.

Of the Lymph and the Lymphatic Vessels.

CHAPTER I.

OF THE LYMPH.

The *lymph* is the fluid contained in the lymphatic vessels; its appearance, as observed by Professors Wutzer and Nasse, and myself, is that of a transparent pale yellow fluid; it has generally no tint of red, unless some of the red particles of the blood are accidentally mixed with it. In the frog it is perfectly transparent, and has not even a yellowish tint. Lymph is devoid of smell, is slightly alkaline, and has a saline taste. The lymph of the intestines, when it contains matter just absorbed from the digested food, is always more or less turbid, and has a yellowish grey or whitish colour, arising from the presence of a great number of globules; it is then called *chyle.*

Analysis of lymph and chyle.—Both lymph and chyle contain albumen and fibrin in the state of solution. The fibrin of lymph removed from the body coagulates in less than ten minutes. Reuss and Emmert* found, by experiment, that 92 grains of lymph of the horse yields only one grain of soft coagulum, consequently less than one-third per cent. of dry fibrin. The fluid which remained after the fibrin had coagulated was evaporated to dryness, and yielded $3\frac{3}{4}$ per cent. of dry residue, consisting chiefly of albumen and chloride of sodium. The fibrin which Reuss, Emmert, and Lassaigne obtained from the lymph of the horse, as well as that which Nasse and I obtained from human lymph, was quite colourless. The fibrin which I procured from the lymph of the frog had always the same appearance as that from human lymph. The pale red colour which Tiedemann and Gmelin ascribed to the lymph, was perhaps produced in the lymph they examined by the accidental admixture of a small quantity of blood.

The following is the composition of the lymph of the horse, according to Lassaigne's analysis:

Water,	92·500
Fibrin,	0·330
Albumen,	5·736
Chlorides of sodium and potassum, with soda and phosphate of lime,	1·434
	100·000

Besides the above ingredients, Tiedemann and Gmelin state that the lymph contains salivary matter, osmazome, carbonates, sulphates, muriates, and acetates of soda and potash, with phosphate of potash.

* Scherer's Journal, v. 691.

The chyle differs from lymph in several particulars. It contains uncombined fatty matter which is not present in lymph. The proportion of the solid ingredients is greater in the chyle; Tiedemann and Gmelin obtained 0·37 parts of dry fibrin from 100 parts of chyle taken from the lacteals of the mesentery of the horse, while from the same quantity of lymph from the lymphatics of the pelvis they obtained only 0·13 parts. The chyle also contains more globules than the lymph, and is more opaque. The globules of the lymph are very few in number, and hitherto have been quite overlooked; Dr. H. Nasse and I have, however, seen them in the lymph of man, and I have seen them repeatedly in the lymph of frogs. It appears that hitherto human lymph had never been examined. The fluid which Soemmering took from "varices" of lymphatic vessels, did not coagulate, and could not have been lymph.

Human lymph.—The rare opportunity of examining the lymph of the human subject occurred to Dr. H. Nasse and myself at Bonn, in the winter of 1832 and 1833. A young man, in the surgical ward of Professor Wutzer, had received, some time previously, a wound on the dorsum of the foot; and a small opening still remained, which it had been found impossible to heal. From the opening lymph constantly exuded, and on passing the finger along the dorsum of the great toe towards the situation of the wound, a quantity of perfectly transparent fluid flowed out each time, sometimes in a jet. This was lymph; for, about ten minutes after it was collected, a delicate coagulum of fibrin (like a spider's web) formed in it.

Microscopic characters.—Being thus enabled to collect lymph in considerable quantity, I was most anxious to know whether it contained any globules. All recent anatomists,—Reuss, Emmert, Sœmmering, Tiedemann and Gmelin, Brande, and Lassaigne,—have failed to observe them: Hewson, however, states that he saw innumerable white bodies, about the size of the nuclei of the red particles of the blood, in lymph taken from the thymus gland; but it is doubtful whether this was really lymph: in lymph taken from the surface of the spleen, and which had a red tint, Hewson states that he found red globules. On examining the lymph obtained as above described, with the microscope, I perceived that, although a clear transparent fluid, it contained a number of colourless globules, which were much smaller and much fewer in number than the red particles of the blood. When the fibrin of the lymph coagulated, a few of the globules were enclosed in the clot; the greater part of them remained suspended in the serum. The coagulum, after it has firmly contracted, consists of a white fibrous tissue; and it can be shown distinctly that it is formed, not by the aggregation of the globules, but by the coagulation of a substance which was previously in solution. On examining, by a high magnifying power, the coagulum of a small quantity of lymph which had been allowed to coagulate in a watch-glass, we

could see the globules of the lymph dispersed through the coagulum, just as they appeared before in the fluid lymph. It was at the thin border of the coagulum that we could best observe the substance which formed it and connected together the globules. It was quite homogeneous, slightly transparent, and, as far as could be observed, did not consist of globules. If it did consist of globules, they must have been much more minute than the visible globules of the lymph.* These observations prove that, although the lymph really contains globules, the fibrinous part of the lymph exists in the state of solution.

Lymph of the frog.—The opportunity seldom occurs for the repetition of these observations on the lymph of man; but, whenever we can procure frogs, the lymph of these animals can always be very easily obtained in a pure state. The skin of the frog, it is well known, is very loosely connected with the muscles; and the nature of the fluid contained between the skin and the muscles is alone sufficient to show that considerable cavities for containing lymph must exist in this situation. If the skin of the thigh is divided, care being taken that no large blood-vessels are cut, and then separated from the muscles for some extent, a clear colourless fluid, of a saltish taste, frequently exudes, but not always. If the frog is very large and recently caught, the quantity of the fluid is very often considerable. In a few minutes it deposits a coagulum of considerable size, which is at first transparent and colourless, and afterwards contracts until it acquires a whitish fibrous appearance.

If the lymph is thus collected from a great number of frogs, sufficient may be obtained for making a more accurate examination of it. By drying the fibrinous coagulum of a known quantity of lymph, and then weighing it, I found that eighty-one parts of frog's lymph contain one part of dry fibrin, a proportion which seems remarkably large. But perhaps we must not attribute much value to an estimate drawn from one experiment, made with so small a quantity of lymph. If frogs are kept for a long time, their lymph ceases to be coagulable; and their blood, in like manner, then yields little or no coagulum.

The lymph of frogs recently caught contains, very scantily diffused in it, globules, which are about one-fourth the size of the red particles of the frog's blood. They are round and not flattened, while the red particles of the blood are elliptic and flattened. In dividing the skin of the frog's thigh, some blood-vessels are necessarily cut; hence some of the elliptic particles of the blood will appear in the lymph when examined with the microscope; their number, however, is so small, that they do not prevent the lymph from being perfectly clear and colourless.

The lymph of the frog and that of man agree so nearly, that, by means of that which may be so easily obtained from the frog, we can at any time demonstrate at lecture the principal qualities of this fluid.

* Compare Dr. H. Nasse's account in Tiedemann's Zeitschrift, v.

Hitherto no medical man could be upbraided if he had never seen lymph, although it is so much spoken of by pathologists and physicians. They have, indeed, been so ignorant of its nature, that the name of lymph has been given to very different fluids. Not merely exudations containing fibrin and albumen, but even the secretions of sores and puriform matters, and especially all matters the nature of which is not exactly known, have been called lymph.

In the lymph of the frog it can be seen, even more distinctly than in that of man, that the coagulum is formed of fibrin which was previously in solution, and that the globules of the lymph have no share in the coagulation. The albumen of the lymph is coagulated by the ordinary reagents. It is remarkable that not only the lymph of the frog is rendered turbid by the addition of liquor potassæ in large quantities, and that albumen is immediately precipitated from the lymph of mammalia on adding liquor potassæ, but that the albumen is precipitated even from a small quantity of the serum of the blood when liquor potassæ is added in large quantity. The liquor potassæ must, however, be quite concentrated.

Colour of the lymph and chyle.—The lymph seems to be colourless in most parts of the body under ordinary circumstances, but it has sometimes been seen of a reddish colour; both Magendie, and Tiedemann and Gmelin, observed this colour in the lymph of animals which had fasted, and in the lymphatics of the spleen the lymph has frequently a red tint. This colour of the lymph of the spleen has been observed by Hewson, Fohmann, and Tiedemann and Gmelin. Seiler perceived it but rarely, and Rudolphi thought it was accidental. I have, however, repeatedly examined the spleen of the ox in the slaughter-house, and, among the numerous large lymphatic vessels which run on the surface of the spleen, have always found some in which the lymph had a dirty reddish colour. Hewson thought that this tint, which is very slight, was dependent on the presence of some red particles of the blood; but I am rather inclined to believe that it is owing to some of the colouring matter of the blood, in the highly vascular tissue of the spleen, having been dissolved by the lymph.

The chyle is almost always more opaque than the lymph of the same animal. The opacity of the chyle seems to be dependent on the globules that it contains. In mammalia, it is generally whitish, particularly after fat or animal food has been taken. In birds, it is not white, and is more transparent. The chyle of the thoracic duct has, in the horse, a reddish tint, which is more rarely seen in other animals. When the red tint exists, it is deepened by exposure to the air.

Nature and source of the globules of the chyle and lymph.—The globules of the chyle of mammalia, at least those of the rabbit, cat, dog, calf, and goat, which I have myself examined by means of the microscope, are not flattened like the corpuscules of the blood; they are globular,

Prevost and Dumas found the diameter of the globules of the chyle to be $\frac{1}{7199}$th of an inch, that is, something more than one-half the size of the red particles of the blood in man.* In examining the globules of the chyle by the microscope, I have always mingled with them, on the glass plate, some of the red particles of the blood of the same animal. I found them in some instances, as in the cat, to be equal in size to the red particles of the blood; in other cases, generally indeed, as in the calf, the dog, and the goat, they are somewhat smaller; in the dog their size is very various,—all are smaller than the red particles of the animal's blood, and the majority of them are very small indeed. In the rabbit, some of the globules of the chyle were larger than the red particles of the blood, although the majority of them were much smaller,—not more than a half or two-thirds the size of the red particle. These minute globules were not finely divided portions of fatty matter, for I had an opportunity of seeing such particles of fatty matter in the chyle of a dog fed with butter, and it was evident that the fatty particles were quite distinct from the true globules of the chyle. Professor R. Wagner's† observations agree with mine. Wagner, also, is very doubtful with reference to the identity of the lymph and chyle globules with the nuclei of the red particles of the blood. Tiedemann and Gmelin have given us the most complete information regarding the chyle; with their observations I cannot at all compare mine, which are much less numerous. One of their statements, however, I must dissent from; they assert very decidedly, that the turbidity and the milky appearance of the chyle depend wholly on the presence of globules of fat suspended in it. They seem to regard the chyle as an incomplete solution of animal matter, in which there are no other globules floating than globules of fatty matter. In fact, they state that by agitating the milky serum of the chyle with ether which was free from alcohol, they were able to render the turbid serum gradually clear. This is a very important point; for if chyle is merely a solution of animal matter, and if with it no other globules are absorbed into the lacteals than globules of fat, there would really be no necessity for the existence of the openings which have hitherto been sought for in vain in the villi of the intestines; and the coats of the minute lacteals, which form the ultimate net-work, might have no larger pores than those to which all animal membranes owe their permeability to fluids, and substances in solution.

But it seems to me to be probable that globules, independent of the more finely divided particles of fat, are really taken up from the intestines into the chyle. On treating the milky serum of the chyle of the cat with ether freed from alcohol, in a watch-glass, the serum seemed at first to become gradually somewhat clearer; but there still remained a

* See E. H. Weber's remarks in Hildebrandt's Anat. t. i. p. 160.

† Hecker's Ann. 1834; Müller's Archiv. 1835, 107.

turbid appearance at the bottom of the watch-glass, even after continuing the experiment a long time with repeated fresh portions of ether. On examining this turbid portion by the microscope I found that it contained the globules of the chyle quite unaltered. I agree with Tiedemann and Gmelin that the chyle becomes more opaque after fat food has been taken; but I cannot allow that all the globules of the chyle are merely particles of fat. Even if ether did render the chyle quite clear, this would not prove that there were no other globules in the chyle than those of fatty matter; for lymph is a perfectly transparent fluid, and yet it has globules diffused through it.

The globules of the lymph must be derived either from particles cast off from the tissue of the organs during the process of absorption, or they must be formed in the lymph itself after it is absorbed. There are no proofs to show that the globules of the chyle are developed in the lacteals. If they are formed in these vessels, it must be in the net-work which is contained in the coats of the intestine, and from which the larger lacteals arise; for I have found the globules even in the chyle taken from those lacteals which run on the surface of the intestines in the calf, in which these vessels, when filled with chyle, are very visible.

The presence of globules in the chyle might be explained even without the necessity of permeation of the coats of the lymphatics, and without pores existing, if Doellinger's hypothesis were adopted. Doellinger* supposes that the villi of the intestines are constantly undergoing solution on their interior, so as to form the chyle of the lacteals, while they are reproduced on their external surface by the aggregation and apposition of particles from the chyle contained in the intestines in the same way as the germinal membrane of the embryo grows by the apposition of the particles of the yolk. There are facts, however, which render this hypothesis improbable. In mammalia the chyle is always more or less opaque after a meal, and is thus distinguished from the lymph—the product of absorption of other parts of the body. The chyle varies, too, according to the nature of the food that is taken. The rapidity with which fluids are absorbed from the intestinal canal is well known; and yet it is scarcely possible that they are conveyed into the blood solely by being imbibed immediately into the capillaries. Colouring matters, too, have been observed a few times in the lacteals, though rarely. The absorption of milk, and consequently of globules into the blood, is rendered in some measure probable by a circumstance noticed by Schlemm. He has observed that, for a certain time after sucking, the blood of kittens is sometimes, but not always, of a yellowish red colour, and separates, when it coagulates, into a red clot and a milk-white serum. Rudolphi and I have verified this observation, and it has

* Froriep's Notiz. i. N. 2.

been confirmed by Mayer.* Rudolphi and Mayer assert that it is the case also in young puppies. I have made the experiment but once on puppies; the result did not confirm Rudolphi's and Mayer's assertion. In young animals it seems, then, that the globules which cause the white colour of the milk are really absorbed into the lacteals. All the milk, of course, cannot be absorbed in this way; for a portion, as Mayer remarks, is coagulated in the stomach. Kastner † repeated Schlemm's experiment without obtaining the same result.‡

CHAPTER II.

OF THE MODE OF ORIGIN AND STRUCTURE OF THE LYMPHATIC VESSELS.

The most important researches of earlier writers on the structure of the lymphatics are contained in the collection of the works of Mascagni, Cruikshank, and others, edited by Ludwig. More recently, this department of anatomy has been much advanced by the distinguished labours of Fohmann,§ Lauth,|| and Panizza.¶

The forms in which the absorbents take their rise may be seen, in preparations of these vessels injected with mercury, to be two:

First, as a net-work, of which the meshes are sometimes oblong, sometimes more uniform [or equal-sided?—gleichförmig]. The meshes are sometimes smaller even than the diameter of the minute lymphatics which form them, so that the net-work is very close, while at the same time the vessels are very irregular in size; and this structure may to the superficial observer have the appearance of aggregated cells, which, however, are merely inequalities and slight dilatations of the vessels, forming a very close net-work. In other parts, where the meshes are larger, the reticulated structure is immediately evident.** The diameter of the vessels varies very much, but they are never so minute as the capillary blood-vessels; and I am acquainted with no absorbent vessels which are not visible to the naked eye. Judging from Fohmann's representations, the lymphatics which he has discovered in branchiæ must be the most minute that are known. It is not at all probable that any more minute lymphatics exist; for the spaces which separate those that we are already acquainted with are very small.

The second form in which the absorbents take their rise is that of small cells, more or less regular, and communicating one with another. Such appeared to me to be the structure of the injected lymphatics of the umbilical cord, and of those of the cornea, the nature of which,

* Froriep's Not. N. 536. 565. † Das Weisse Blut. Erlangen, 1832.

‡ A farther account of the chyle is given in the section on Digestion.

§ Das Saugadersystem der Wirbelthiere. i. Heft. Heidelberg, 1827, fol.

|| Essai sur les Vaisseaux Lymphatiques. Strasb. 1824. Ann. des. Sc. Nat. t. iii.

¶ Osservazioni Antropo-zootomico-fisiologiche. Pavia, 1833.

** See Plate i. figs. 7 and 8.

however, is doubtful. This was also the appearance of the lacteals in the calf, which I injected by forcing the mercury into one of the trunks which were issuing from the intestines, filled with chyle, in a retrograde direction, so as to overcome the resistance offered by the valves. I succeeded tolerably well in one case by forcible injection. The great number of cells which are by this means filled with mercury suggests the idea that the absorbents take their rise in the cells of the cellular tissue itself. Fohmann,* indeed, is of opinion that what we call cellular tissue consists merely of lymphatic vessels. This, however, appears to me very doubtful. The identity between the cells that I have described and lymphatics is more especially problematical in those parts in which the cells are more particularly met with, and in which none of the long and regular lymphatic vessels occur, as is the case in the umbilical cord and cornea. From having compared good injections of lymphatics with other specimens in which the injection has not succeeded so well, and from some experiments of my own, I am inclined to believe that many of what are called the cellular lymphatic radicles are not really lymphatics, and that the general form in which the radicle lymphatics exist even where these vessels are most numerous, is that of a close and often regular net-work.

Although I cannot but greatly admire the beautiful injected specimens of the absorbents by the excellent Fohmann, which I have seen repeatedly in the museum at Heidelberg,—and I confess that these preparations excel everything of the kind that I have seen,—nevertheless, I can perceive a very distinct difference between the many perfect injections and a few which are not so good, and doubt if everything that is shown by injection consists of lymphatic vessels. Thus, I cannot think that the appearances produced by injection of mercury under the corneal conjunctiva, and between the layers of the cornea, are owing to lymphatics. With regard to the lymphatics of the umbilical cord described by Fohmann,† I am quite in doubt. I injected the cord according to Fohmann's directions, and succeeded, even in a six months' fœtus, in filling parts of the cord with mercury so well, that I could keep the preparation. Numerous small cells of $\frac{1}{101}$th to $\frac{1}{254}$th of an inch in diameter became filled with quicksilver. These cellules are certainly not formed artificially; the majority of them are nearly equal in size, and the mercury passes from one cell to another without any extravasation. The greater part of the tissue of the cord around the blood-vessels is formed by them. It was only just at the umbilical insertion of the cord that the mercury filled several very short parallel canals. I know not whether these cells are lymph cells, and am certainly sceptical as to their being absorbing organs.

Do the lacteals commence by open mouths?—The lacteals of the small

* Tiedemann, Zeitschrift fur physiologie, iv. 2.

† Loc. cit.

intestines arise partly in the villosities; but they also commence in the whole surface of the mucous membrane of the intestinal canal. When the lacteals are injected with mercury, none of the metal escapes from the surface of the mucous membrane. The villi also are not perforated at their extremity, as Lieberkühn, Cruikshank, Hedwig, and Bleuland incorrectly supposed.*

I have found that if a portion of fresh sheep's intestine, removed with the mesentery, and tied at one extremity, is strongly distended with milk by means of a syringe, the lacteals immediately become filled; and the milk moves very rapidly through them; for if any of the lacteals are emptied by pressing onwards their contents, they are seen to re-fill immediately with milk from the intestine, particularly if the intestine is compressed at the same time. If the passage of the milk into the lacteals in this experiment is effected without any previous laceration of the mucous surface, it would be an important fact. The injection of the lacteals with milk takes place most rapidly when the portion of intestine is pressed at its extremities, as if trying to diminish its length; the phenomenon is not so rapid when the compression is applied laterally. If, instead of milk, fine injection coloured with vermilion is used, the absorption takes place very slowly; and mercury cannot in this way be made to enter the lacteals at all. But with solutions of colouring matters which are perfectly soluble, such as indigo, the lacteals of the mesentery may by this method be very easily injected. In every case, however, in which the lacteals become injected by this procedure, there seems to be laceration of the mucous membrane at some point, for the lacteals fill suddenly; and, on examining afterwards the inner surface of the intestine, there is frequently found a spot here and there, where the mucous membrane has lost its integrity. Consequently I attribute no importance to these experiments in reference to the question of the existence of openings in the extremity of the villi. I observed the phenomenon in no other animal than the sheep.

It still, however, remains an undecided question whether the globules of the chyle enter the lacteals already formed. The varying opacity of the chyle, according to the difference of the food taken, is the chief argument in favour of their being taken up from the cavity of the intestine, and not afterwards formed in the lacteals. But where are the openings by which they enter these vessels?—for they must require larger pores than those by which all soft tissues, and even the walls of the capillaries, are rendered permeable to water and matters in solution, but which are too minute to allow the escape of the red particles of the blood from the capillaries. All good observers agree that there are no visible openings in the villi of the intestines; and I have myself repeatedly ex-

* See Rudolphi, Anatomisch-physiol. Abhandlungen, and Albrecht Meckel, in Meckel's Archiv. t. v.

amined the villi of the intestines of the calf, ox, rabbit, hog, and cat, without having even perceived any perforation in their extremity. No opening certainly exists at that part of the villi.

Structure of the intestinal villi.—The villi of the intestines are short processes, a quarter of a line to a line, or at most a line and two-thirds in length, rising from the surface of the mucous membrane, and giving this membrane, when magnified, the appearance of a thick fleece. Their form is sometimes cylindrical, sometimes lamellar, and frequently pyramidal.

This is their character, however, as a general rule only in man, most mammalia, and many birds. Something similar is observed in a few fishes; and in a serpent, the python bivitatus, Retzius has described processes of the mucous membrane of the intestine, which resemble villi, and can scarcely be considered as anything else; although Rudolphi has said that fishes and reptiles have no true villi. A. Meckel is incorrect in characterising all villi as lamellæ broad at the base and narrowed at their free extremity. It is true that they are flattened in most mammalia, as in the rabbit, dog, and hog; but in the calf, ox, and sheep, many of the villi are cylindrical; and sometimes, as in the sheep and ox, the flattened villi are more numerous in one part of the intestines, in another the part cylindrical; and in the two last-named animals, particularly in the sheep, the villi in many parts of the intestines are flattened and broad, with cylindrical tips. By the villi becoming broader at their base, and being connected with each other so as to form folds, a gradual transition is established from the villi of mammalia to the rugæ or folds by which they are replaced in many birds and in reptiles. This transition is sometimes perceptible in the intestines of one and the same animal. Thus, in the rabbit, the pyramidal villi at the upper part of the small intestine are united at their base into folds, while in the middle portion of the same intestine they are more separate. The free extremity of the villi is sometimes rounded, sometimes rather pointed, and at other times, as in the dog, it is as it were truncated.

Rudolphi at first believed that the villi were devoid of blood-vessels, and A. Meckel imagined that all the injection which entered them did so by imbibition or extravasation. Meckel could not have had before him good preparations of injected villi when he came to this conclusion. Not only can the vessels of the villi be beautifully shown by injection, as Doellinger, Seiler, and Lauth have described and represented, but I have, with the naked eye as well as with a lens, seen them filled with blood. Once I observed this in the calf, and afterwards in the dog, the intestine being examined immediately after death before it was washed.

The extremity of the villi presents the same delicate texture as the rest of their surface. The assertion of Bleuland and others, that they had an opening at their extremity, was refuted by Rudolphi, who expressed

all that has hitherto been known of the structure of these parts in the following words:—"They have never any visible opening; in their interior there is a net-work of blood-vessels, which can seldom be demonstrated, however, except by injection; the net-works of lacteals also take their rise in the villi."

It appears to me to be an important circumstance, that the villi are in part hollow, and are formed of an exceedingly delicate membrane in which blood-vessels ramify. The simple cavity I have found principally in the cylindrical villi. In examining, while it was quite fresh, the intestine of a calf, the lacteals of which were white with chyle, I was surprised to find the villi filled with the same white opaque matter. On another occasion I found the villi of the small intestine of the same animal not filled with white matter, but empty and distinctly hollow, which Rudolphi himself had once observed in a young pig. In the calf, and in the ox also, I was able, by means of a needle, to lay open the delicate cavities of the villi. The lamellar and rather broad intestinal villi of the rabbit also appeared to me to be hollow. A. Meckel once saw the appearance of a cavity in the villi, and has given a drawing of it; but he supposed it to be produced by a folding of the membrane: which was certainly not the case in the villi which I have observed. By comparison I have ascertained that the thickness of the membrane which forms the villi in the calf is $\frac{1}{530}$th of an inch, and the diameter of the capillary blood-vessels which run in this membrane may be reckoned at from $\frac{1}{3700}$ to $\frac{1}{1850}$ of an inch. I was able easily to convince myself of the existence of a cavity in the villi of the intestine in the calf, ox, sheep, and goat, and more easily in the narrow or really cylindrical villi, than in those which were flattened and broad; but in the villi of the cat, hog, and dog, I did not see the cavity satisfactorily; the villi in the dog seem to be hollow only in their upper part. The closely arranged plaits in the intestine of fishes,—the eel, carp, and clupea alosa,—have likewise no cavity; they are solid folds. The flat broad villi, also, which are met with at certain parts of the intestine of the sheep, as well as the similar quite broad villi of the intestine of the rabbit, evidently do not contain one single cavity; in all broad flat villi the lacteals seem to arise by more than one simple cavity. An opportunity occurred, at the dissecting-rooms in Berlin, of examining the villi of intestines in which the lacteals were filled with chyle in the human subject. They were found to contain a simple cavity running from base to apex. This was proved both by the microscopic examination of the villi by Henle, and by their injection with mercury by Schwann, who forced the mercury into the lacteals which were distinctly visible in the mucous coat, and thus filled the villi even to their closed extremity.*

* There is something of a very different nature, which might be mistaken for hollow villi. This is a kind of epithelium, but of extreme delicacy. Rudolphi first men-

In the experiment already mentioned, in which the lacteals are injected by distending the cavity of the intestine with milk, villi filled with the milk may likewise be detected at some points. The experiment must be made very often before this accidental injection of the villi takes place. It is probable that the milk finds its way into the villi, not through the intestinal surface of the villi, but in a retrograde course from the net-work of lacteals which the milk had previously entered through lacerations of the mucous surface. When such villi, filled with milk, are examined with the microscope, the narrow cylindrical villi appear to contain one single canal, while in the broad flat villi several irregular anastomosing canals are seen directed, for the most part, from the base to the free extremity of the villosity, there ending in a blind extremity, or continued into the digitated processes with which the flat villi are terminated. The canals in the flat villi lie close together, forming a very irregular net-work; they exceed considerably the usual size of the capillary blood-vessels.

[Professor Krause of Hanover* has lately had an opportunity of seeing the lacteals in the villi of the jejunum, beautifully filled with chyle, in the body of a young man who had been hung soon after taking a full meal of farinaceous food. The lacteal that issued from each villosity arose by several smaller branches, of which some terminated by a free extremity, others anastomosed with each other.]†

I have never perceived any opening at the extremity of the villi, and in my earlier examinations of them I could see no appearance of foramina on any part of their surface. But I have lately observed, in portions of the intestine of the sheep and ox, which had been exposed for some time to the action of water, that over the whole surface of the villi there were scattered very indistinct depressions, which might be regarded as oblique openings. However, I mention this observation with great hesitation and distrust. The villi must be examined with a simple microscope, and must be under water on a black surface.

Structure of the intestinal mucous membrane.—The villosities of the intestines, whether they have or have not open mouths on their surface, cannot possibly be the sole organs for the absorption of the chyle, for in

tioned the epithelium as existing in the badger. In calves and kittens there is no difficulty in detecting a delicate unorganised membrane, which can be easily stripped off from the villi, like a glove. It is so very soft and friable, that if the intestine is much washed before it is examined, it will have separated of itself. In oxen it is still more delicate, and is not easily seen; when the intestine is washed, it separates from the mucous membrane in the form of a mucous substance, in which the form of the villi is only here and there perceptible. It is very different from the solid epithelium of other mucous membranes. It is not solid, like an epidermis; on the contrary, although coherent in a membranous form, it is so nearly allied to mucus, that it seems to me to be a secretion intermediate between epithelium and mucus.

* Müller's Archiv. for 1837. Heft i. p. 5.

† See plate i. fig. 9.

many animals they do not exist. This consideration led me to examine the mucous membrane itself from which the villi are processes, and which is common to all animals.

If in a well washed portion of the small intestine of any mammiferous animal we examine the structure of the membrane by which the villi are connected at their base, by means of a simple microscope, we perceive, without much difficulty, an extraordinary number of very small openings, which are about twice or three times as large as the red particles of the blood of the frog, and eight or ten times as large as the same bodies in mammalia. These minute openings are in mammalia sometimes so close and numerous, that the portion of membrane which separates them is scarcely as broad as the openings themselves; generally, however, they are more widely separated; and in this case they give a spongy and exceedingly soft appearance to the membrane. The basis of the villi even appears in sheep and oxen, as it were beset with these foramina. They are the openings of Lieberkühn's follicles.*

The observations of Fohmann, in whose most perfect injections of the lacteals of the intestine of fishes the mercury never escaped on the inner surface of the intestine are opposed to the notion of the lacteals arising by open mouths so large as to be visible by the microscope,—a notion which is disproved likewise by the fact of Schwann having, as above mentioned, filled single villi of the human intestine with mercury injected from lacteals in the mucous membrane.

The absorbent glands are in birds almost wholly wanting, except in the neck; and in reptiles and fishes they do not exist at all. In these animals they seem to be replaced by mere plexuses of absorbent vessels. The glands themselves consist, in fact, merely of reticulated anastomoses and interweavings of the vessels. The vasa inferentia of an absorbent gland divide on entering it into small branches, and by the reunion of small branches are formed the vasa efferentia, which are less numerous, and somewhat larger than the vasa inferentia. In consequence of the free anastomosis of the two sets of vessels,—those entering and those leaving the gland,—so as to form a net-work of absorbents, of which the gland is constituted, we are enabled to fill the lymphatics issuing from the gland with mercury forced into those which enter it. The simpler absorbent glands resemble mere plexuses of absorbent vessels; but one of the larger glands, when filled with mercury, has a cellular appearance. But even these apparent cells seem to be merely small dilatations of convoluted vessels; the net-work of absorbents in other parts has also frequently a cellular appearance; the small spaces between the vessels not being distinguished without careful observation. The passage of mercury through the glands when the absorbent vessels

* See Boehm, De Gland. Intestinal. Struct. Berol.

going to them are injected is in favour of this opinion. The opposed opinions of Cruikshank, who admitted the existence of cells in these glands, and of Meckel, Hewson, and Mascagni, who regarded these apparent cells as dilatations of the convoluted absorbent vessels, can be easily reconciled.

Abernethy found the mesenteric glands in the whale of a saclike (?) structure; while, in the dolphin, according to Knox, they are solid.*

Structure of the absorbent vessels.—It is very certain that the coats of the absorbents in the absorbent glands, as well as in other parts, are traversed by capillary vessels; even the lacteals on the intestines, according to Fohmann's examination, possess an internal coat, which extends as far as the net-work from which they take their rise; and it has been already mentioned that the capillary vessels in the villi are very numerous. Consequently, even the absorbents, which form the radicle part of the system, are to be regarded as organs of very complicated structure, into which capillary vessels enter as elementary parts. The lymphatics, with the exception of the net-work by which they commence, are formed of two coats,—an external smooth coat, and an internal one, which forms valves, by the arrangement of which the flow of the lymph towards the larger trunks of the lymphatic vessels is favoured, and its reflux in the opposite direction impeded.

We have now to enquire whether absorbent vessels at their origin, or in any part of their course, have any communication with canals of other kinds besides that with the venous system, by means of the trunk of the absorbent system,—the thoracic duct.

Do the absorbents communicate with secreting canals of glands?—Cruikshank, J. F. Meckel, the elder, and Panizza, have observed, in injecting the lactiferous ducts of the mammary gland, and the ductus hepaticus, with mercury, that the metal passed likewise into the lymphatics. Walter also filled the lymphatic vessels from the bile-ducts of the liver. It must not, however, hence be concluded, that the lymphatics at their origin have open communications with the secreting canals of the glands. Recently, in injecting the mammary glands of a bitch, I also found that the surrounding lymphatics became filled, but the cases in which this took place were those in which the vesicular extremities of the lactiferous ducts were not well filled with injection; extravasation had, in fact, taken place, and, that being the case, the injection could find its way into no parts so readily as into the lymphatics, on account of their being so much larger than the capillary blood-vessels. If any open communication between the lymphatics and secreting canals really exists, which Panizza denies,—and certainly with justice,—it could only be between the lymphatics and the trunks of the secreting canals; for

* Froriep's Notiz. N. 158.

the lymphatics which form the net-work by which the larger lymphatic vessels take their rise, are many times larger than the blind extremities of the secreting canals of the conglomerate glands. The *connection of lymphatics and arteries,* of which Magendie speaks so cursorily, is not better proved.

The *connection of the lymphatics with the small veins,* however, has been again rendered a subject of controversy, in consequence of Fohmann's observations.

Fohmann, Lauth, and Panizza, have discovered between the lymphatics and the veins of the thigh and pelvis in birds, communications which are visible to the naked eye. I will presently describe the connection which I have discovered between the lymphatics of the thigh and the ischiadic vein in the frog. But this communication of the larger trunks is very different from a communication of single lymphatic vessels with minute veins, which Fohmann asserts to exist in birds, reptiles, and fishes, and of which he has given representations. Fohmann admits, that in man and mammalia, which have lymphatic glands, this communication of the absorbents with the veins does not exist, except in the glands. The statements of Lippi* concerning the communications of the lymphatics and veins, and his representations of them, have been shown by Fohmann† and Panizza to be undeserving of much confidence. Fohmann, however, maintains that the veins and absorbents do communicate in the lymphatic glands, as had been observed by J. F. Meckel, the elder, and Ph. F. Meckel when injecting the absorbent vessels with mercury. When mercury is forced into the vasa inferentia of an absorbent gland, the veins arising from the gland become filled, as Beclard also observed, very readily—often indeed much sooner than the efferent absorbent vessels. This led Fohmann into an error. On injecting in the seal the vasa inferentia of that mass of absorbent glands which in the dog and dolphin is called "pancreas Asellii," he observed, that when the glands were filled, the veins which arose from them, but no efferent absorbent vessels, became injected; he thence concluded that this mass of glands has no other efferent vessels than the veins.‡ This error was corrected by Rosenthal,§ who found that in the seal all the lacteals enter this mass of glands, and that one large efferent absorbent—the ductus Rosenthalianus—issues from it. And in the dog and dolphin Rudolphi has seen a number of vasa efferentia issuing from this mass of glands.|| Ro-

* Illustrazioni fisiologiche e pathologiche del sistema linfatico-chilifero, etc. Firenze, 1825. † L. c. p. 4.

‡ Fohmann, Anat. Untersuch. über die Verbindung der Saugadern mit den Venen. Heidelberg, 1821.

§ Froriep's Not. ii. p. 6. Rosenthal's representations of the organs are to be found in Nov. Act. Nat. Cur. t. xv. p. 2.

|| See Rudolphi's remarks on this subject in his Physiologie, 2 bd. 2 abth. pp. 241—250.

senthal's observations have been confirmed by Knox.* But, although Fohmann was wrong in supposing that in this case all the matter brought to the gland by the lacteals was conveyed away by the veins, still the fact remains, that mercury passes with extreme facility from the lymphatics into the veins of the glands. Schroeder Van der Kolk observed the veins of absorbent glands, injected from the vasa inferentia, become filled without any of the mercury passing into the thoracic duct.† Panizza‡ injected a gland from two vasa inferentia, and observed that the mercury passed from one wholly into the veins of the gland, and from the other into the efferent absorbent vessel. Gerber and Alb. Meckel§ also remarked the facility of communication from the absorbents to the veins. A. Meckel, however, as well as Rudolphi and E. H. Weber, doubt that this proves any real communication between the two sets of vessels. A. Meckel states, as a reason for his questioning the existence of a real communication, that, when the seminal duct of the epididymis of the dog is injected, the veins are also filled. I also doubt very much the existence of an actual open communication between the lymphatics and minute veins in the glands; and the circumstances which induce me to doubt it are, that, when glands are injected from their excretory duct, the small veins of the gland also frequently become filled with the mercury, and that the cases in which this occurred to me were always those in which the ducts had not been well filled,—their acini not distended; and, lastly, that similar extravasation takes place from the ducts of the mammary gland into the lymphatics of the gland, and this likewise in cases where the acini of the mammary gland are not well injected. The coagulated lymph in the absorbent glands resists the passage of the mercury; the substance of the gland is lacerated; and the coats of the lymphatics being supplied with capillaries which are continuous with veins, the rupture of one lymphatic in the interior of a gland must be attended with laceration of capillary vessels and veins.

In the same manner, also, as E. H. Weber observes, fluids find their way very easily from the branches of the pulmonary artery into the bronchi, although no natural communication exists between them. I regard, in the same light, the passage of injection from one order of vessels into another,—from blood-vessels into the secreting canals, and from the secreting canals into blood-vessels,—in the secreting glands.‖ If, however, I should ever see a direct communication of a lymphatic external to the glands with a small vein, I would acknowledge it as a thing

* Edinb. Med. Surg. Journ. i. July 1824. Froriep's Not. 158.

† Luchtmans, De absorptionis sanæ et morbosæ discrimine. Traject. ad Rhen. 1829.

‡ Loc. cit. p. 56.

§ Meckel's Archiv. 1828, p. 172.

‖ On the question of the communication of the lymphatics and veins, see E. H. Weber's observations in Hildebrandt's Anat. t. iii. pp. 113—121.

evident to the sight, without, however, admitting the existence of such communication in the interior of a gland, where it is invisible.

Terminations of the absorbents. — Since the communication of lymphatics with small veins has not been observed in man and mammalia, the absorbent and venous systems can be regarded as connected only by the principal lymphatic trunk, the thoracic duct, which opens into the left subclavian vein, and by smaller lymphatic trunks which pour their contents into the internal jugular and subclavian veins of the right side. All other communications between the absorbents and the great veins seem to be exceptions merely to the normal structure; such was the case witnessed by Professor Wutzer and myself, in which a branch was given off from the thoracic duct and immediately entered the vena azygos.* This branch is worthy of notice, however; for Panizza has found that in the hog a regular communication exists between branches of the thoracic duct and the vena azygos.†

Lymphatic hearts.— No motions having hitherto been observed in the lymphatic system, my discovery of small pulsating sacs connected with the lymphatic cavities in frogs is doubtless important. These organs must be regarded in some respects as hearts of the lymphatic system. I have found two pairs of them in the frog; one situated just under the skin in the ischiadic region, the other more deeply over the third cervical vertebra. The pulsations of these sacs are quite independent of those of the heart, and continue when the heart is removed from the animal, even after the body of the animal is cut in pieces; the pulsations of the cervical pair are not always synchronous with those of the pair in the ischiadic region, and even the corresponding sacs of opposite sides are not always synchronous in their action. They contract about sixty times in a minute. They contain colourless lymph; and the lymphatic vessels, and lymph spaces of the extremities, can be inflated from them. When air is forced into the inferior lymphatic heart, the lymphatic trunks and the lymph spaces under the skin and between the muscles of the thigh become distended, as well as a superficial lymphatic running along the back. In a few instances a delicate vessel which accompanied the abdominal aorta also became inflated. When the air was forced into the superior or cervical lymphatic heart, the lymph spaces of the axilla became inflated. The inferior lymphatic heart on each side pumps the lymph into a branch of the ischiadic vein. By the superior, the lymph is forced into a branch of the jugular vein, which becomes turgid each time that the sac contracts. The vein passes forwards, receives a branch from the occiput; the jugular vein then descends, receives a vein from the larynx, and at length opens into the vena cava superior. Similar pulsating organs seem to exist in all reptiles. I have hitherto discovered the

* See Wutzer in Müller's Archiv. 1834.

† Compare Otto, Patholog. Anat. p. 366.

superior pair only in the frogs and toads. The inferior pair I have found in the salamanders and lizards; in these animals they are situated at the sides of the root of the tail behind the ilium, and are more difficult to find than in the frog, where they lie immediately under the skin.* Panizza has discovered the inferior pair of these lymphatic hearts also in serpents.†

CHAPTER III.

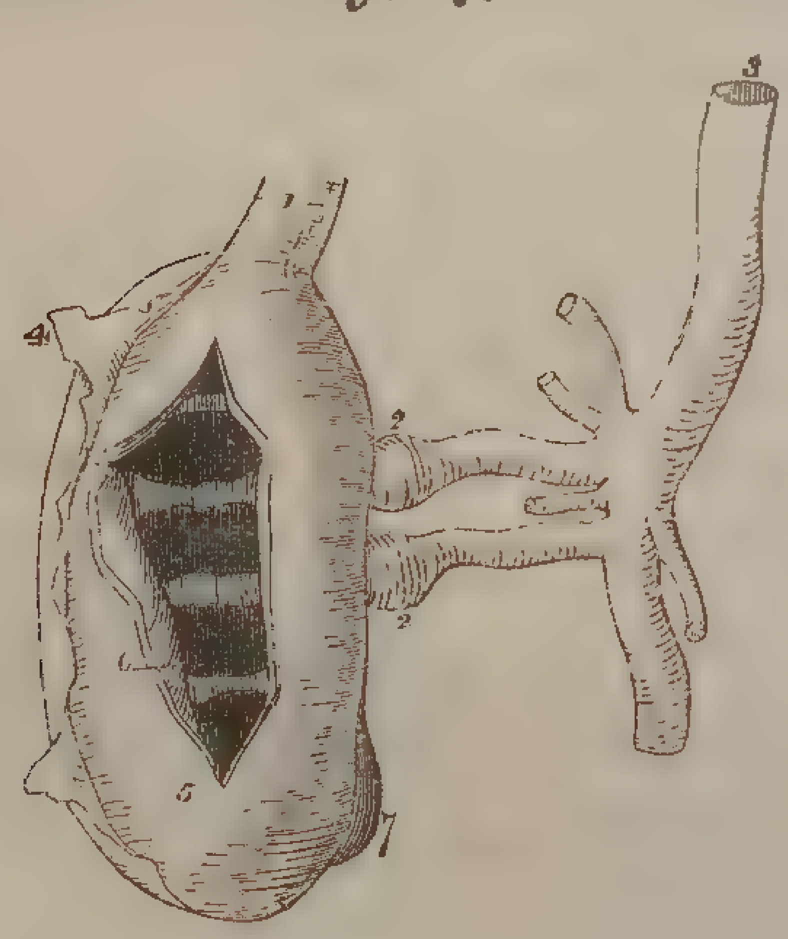
OF THE FUNCTIONS OF THE ABSORBENTS.

During the circulation of the blood through the minute capillary vessels, the red particles exert a vivifying influence on the parenchyma, and at the same time undergo a change of colour; but they can be traced in their course into the veins,—they are not retained in the tissue. The fluid portion of the blood, however, with the fibrin and albumen in solution, like every fluid matter, is capable of permeating the walls of the capillaries, and of being imbibed by the particles of the tissue contained in the meshes of the capillary net-work through which the blood is flowing. The dissolved ingredients of the blood thus imbibed by the parenchyma must serve the purposes of nutrition and secretion. Hence it is that venous blood contains less fibrin than arterial blood.‡ The fluid portion of the blood, therefore, will be imbibed by the tissues in considerable quantity, and what remains after the purpose of nutrition is fulfilled will collect in the net-work of lymphatics, which occupy in all parts of the body the interstices of the proper tissues of the organs; a direct com-

* Philos. Transact. 1833, p. 1. Poggend. Annal. 1832. Hft. viii.

† [Professor E. H. Weber has given a very accurate description of the lymphatic

Fig. 17.



hearts in a large species of serpent, the python bivitatus. Each heart (fig. 17) is about nine lines in length and four lines in breadth, has an external cellular coat (fig. 17, 4), and a thick muscular coat (fig. 17, 5); four muscular columns running across its cavity, which communicates with three lymphatics (fig. 17, 1,—only one is here seen), and with two veins (fig. 17, 2, 2). All the orifices are provided with valves formed by duplicatures of the smooth membrane that lines the cavity (fig. 17, 5) of the heart. The heart lies in a kind oft horax formed by the last rib, and by the transverse processes of the last lumbar and first sacral vertebra. The motions of the tail produce dilatation and contraction of this thorax, and Prof. Weber believes that these motions aid the heart in pumping the lymph into the vein (fig. 17, 3), which conveys the blood to the kidney. Each heart has, at its inner border, a small appendage or auricle (fig. 17, 7), the cavity of which is in no way separated from that of the rest of the organ.]

‡ See page 114.

munication between the capillaries and lymphatics by means of vasa serosa is not needed for the passage of the fluid parts of the blood into the lymphatics, and indeed no such communication has been proved to exist.

The fluid part of the blood having supplied the materials for the nutrition of the tissues, is again returned to the circulation by the lymphatic vessels. The lymph consequently must, in its composition, be exactly identical with the fluid portion of the blood or liquor sanguinis, and the blood itself must consist merely of lymph and red particles. An observation which I have made, and which can be easily repeated, is sufficient to prove that the fluid contained in the lymphatic vessels is formed principally of the fluid parts of the blood, and is not a perfectly new fluid. I have observed that when the blood of the frog does not coagulate, the lymph also does not coagulate. Thus, when frogs have been kept out of water for eight or more days during the summer, their blood often loses its property of coagulation, and under such circumstances the lymph taken from the lymph cavities of the same animal affords no coagulum. Thus the peculiar state of the fibrin, or its absence in the blood of the frog at certain times, determines the very same state of the fibrin in the lymph, or its absence from that fluid.

1. *Of the absorption by the lymphatics and lacteals.*

Proofs that they absorb.—It might at first appear doubtful whether the lymphatics and lacteals do really absorb, were it not that the lymph contains peculiar particles or globules, that absorption by the lacteals is a well ascertained fact, and that the colour of the chyle varies, becoming more white or more opaline according to the food taken. There are circumstances, however, which prove the fact of absorption by lymphatics in other parts. It is not merely that the lymphatics often become painful, that red streaks appear in their course, and that the neighbouring lymphatic glands become swollen after the application, by friction, of irritating matters to the skin; the lymphatics around collections of peculiar animal fluids have been seen filled with these fluids. I attribute no importance to the somewhat extravagant assertions of Mascagni, who states, that in animals which died from pulmonary or abdominal hemorrhage, the lymphatics of the pleura and peritoneum have been seen filled with blood. But Assalini, Saunders, Mascagni, and Soemmering have all observed bile in the lymphatics coming from the liver in cases where the bile ducts were obstructed.* Tiedemann and Gmelin also, after tying the ductus choledochus in dogs, found the lymphatics of the liver filled with a fluid of a deep yellow colour; the lymphatic glands which these lymphatics passed through were yellow, and the yellow fluid taken

* See Weber in Hildebrandt's Anat. iii. p. 123.

from the thoracic duct contained the components of the bile.* Lymphatics around osseous tumours have been found to contain calcareous matter.†

Absorption of pus.—Magendie,‡ who questions the absorbing power of the lymphatics, relates the following case observed by Dupuytren. A woman, who had a very large fluctuating tumour on the inner side of the thigh, died in the Hôtel Dieu. A few days before her death, inflammation had attacked the subcutaneous cellular membrane of the thigh. On dividing the skin over the tumour, Dupuytren saw some white points appear in the lips of the incision, and in the subcutaneous tissue white lines were visible, which were found to be lymphatics filled with pus. The inguinal glands were filled with the same matter, but no traces of it could be discovered in the lumbar glands or thoracic duct. Magendie also mentions another case which occurred at the Hôtel Dieu: in consequence of compound fracture, a large abscess had formed, and here pus was found in the veins and lymphatics which arose from the part. On the other hand, Andral has examined, repeatedly, the lymphatics in the neighbourhood of abscesses, but never found any filled with pus. Pus contains globules, which are larger than the red particles of the blood; in part twice as large, according to Weber; consequently the same question arises here as in reference to the absorption of the globules of the chyle. The entrance of the globules of pus into the lymphatics presupposes the existence of apertures of corresponding size in these vessels. In the parenchyma of organs where there is no free surface, no such apertures can exist. The fluid part of the pus may be easily absorbed into the lymphatics, but the presence of the globules of the pus in these vessels appears to me to be quite independent of absorption. I should regard them rather as the product of inflammation of the lymphatics themselves, or suppose that they have entered mechanically in consequence of solution of continuity of the lymphatics involved in the disease. When pus is found in the blood,—for instance, in the veins,—it is generally the product of inflammation in these veins themselves; or it is pus which has found its way mechanically into the capillaries which have suffered solution of continuity in consequence of the suppuration. Thus, for example, after amputation, the pus of abscesses in the stump may find its way into the blood-vessels independently of absorption, or pus may be formed in the interior of the principal vessels divided in the amputation, in consequence of inflammation of these vessels. Pus being matter which has lost its healthy organic composition and properties, its presence in the veins gives rise to fresh deposition and inflammation; thus are produced abscesses in other parts of the body, as is not unfrequently observed in consequence of great suppurations, and during the existence of suppurat-

* Die Verdauung nach Versuchen, ii. 40. † Otto, Patholog. Anat. i. 372.
‡ Magendie's Physiologie, ii. 21. Milligan's translation, p. 522.

ing wounds after amputation; numerous abscesses in the lungs, liver, muscles, and other parts often occurring under such circumstances. It can scarcely be imagined that the pus in these abscesses had been absorbed.* The presence of pus in the blood causes inflammation and abscesses in other parts, but is never followed by the secretion of pus with the natural secretions; for example, with the urine. It is, in my opinion, impossible for pus to be separated from the blood by secretion in the kidneys. The proximate principle of the pus may be separated in this way, but the globules of the pus cannot; for no kind of globules can permeate the walls of the capillary vessels. If it has ever occurred that, in consequence of suppuration in some other part, pus has been suddenly discharged with the urine from the kidneys, it could only have been by the pus having found its way into the blood, and thus excited inflammation and abscesses in those organs. A sediment in the urine, not properly examined, is often mistaken for a metastatic secretion of pus from the kidneys.

Absorption of foreign substances.—Magendie first denied the absorbing power of the lymphatics. Hunter had asserted that coloured water injected into the abdomen of an animal is soon discoverable in the lymphatics. Flandrin has made the experiment in horses without success; and Magendie assures us that with M. Dupuytren he repeated similar experiments more than one hundred and fifty times, and never found any of the substances absorbed in the lymphatics. On the other hand, Mayer and Schroeder van der Kolk observed an evident, though slow, absorption of foreign matters from the intestinal canal by the lymphatics.

The Academy of Philadelphia, as well as Lawrence and Coates, witnessed the absorption of prussiate of potash; but according to the observations of the Academy colouring matters were not absorbed. Hallé and others, after the introduction of colouring matters, could not detect them in the thoracic duct, while they had evidently entered the blood and the circulation.†

The result of most experiments is, that salts are the only foreign matters absorbed by the lymphatics. Thus the numerous experiments of Tiedemann and Gmelin, cited at page 240, show that colouring matters introduced into the intestinal canal are not taken up by the lacteals, although they are afterwards found in the blood and urine. Salts were the only foreign substances that they could detect in the chyle, and these but few times; thus, only once out of many times, were they able to detect iron in the chyle of a horse to which sulphate of iron had been given, and prussiate of potash, and sulpho-cyanate of potash, each once in

* See the excellent remarks of Cruveilhier in the article Inflammation of the Veins, in his Anatomie Pathologique.

† See also Tiedemann and Gmelin, Versuche über die Wege, &c.

the chyle of dogs. To these I may add an experiment of my own. I placed a frog with its posterior extremities in a solution of prussiate of potash which reached nearly as high as the anus, and kept it so for two hours. I then washed the animal carefully, and, having wiped the legs dry, tested the lymph taken from under the skin with a persalt of iron, the lymph assumed immediately a bright blue colour, while the colour of the serum of the blood was scarcely perceptibly affected by the test. In a second experiment, in which the frog was kept only one hour in the solution, the salt could not be detected in the lymph.

Peculiarities of the lymphatic and lacteal absorption.—The conclusion which must be drawn from a consideration of all these facts, is, that the lymphatics do really absorb, but that their absorbing action is confined to particular fluids, for which perhaps they have an affinity: some foreign matters, such as salts, are taken up by the lymphatics, although with difficulty; while others, such as colouring matters, are generally not absorbed at all. The matter which the lymphatics are ordinarily engaged in absorbing is the liquor sanguinis, which during the circulation of the blood through the capillaries is imbibed by the tissues. Besides this fluid, however, small molecules are taken up from the parenchyma of the organs and form the globules of the lymph, in the same manner as the globules of the chyle are, as it appears, absorbed by the lacteals with the fluid portion of the chyle from the food contained in the alimentary canal.

The organic process by which the lymphatics absorb is, therefore, materially different from that by virtue of which the capillaries imbibe all foreign matters which are in a state of solution; it is also different from the process of absorption in the radicle fibres of plants, by which every matter which is in solution is absorbed.*

By simply comparing the chyle taken from the lymphatic system with the chyme in the alimentary canal, it will be at once seen, that the absorbents do not merely absorb, that they also produce a change in the matter which they take up. The new nutritive matter derived from the food does not acquire its property of coagulating spontaneously until it is contained in the absorbent system of vessels, and this property becomes the more marked the further the chyle has advanced in these vessels. It is possible that the lymphatic vessels in other parts of the body have the same power of converting the albumen into coagulable matter. It is at any rate evident, that this action of the absorbents on the matters absorbed distinguishes completely the vital action exerted by them from imbibition, and from the process by which all matters in solution are received immediately into the capillaries. It is probable, as E. H. Weber has endeavoured to prove, that the absorbents produce a change in the composition even of foreign matters

* Tiedemann's Physiol. i. 223. English Translation, p. 85.

which they take up. Thus Emmert has observed, that, after the abdominal aorta had been tied, the poison of the angustura virosa inserted into a wound of the foot, did not exert its deadly effect, and that prussic acid applied in the same way had also no effect on the animal, when the circulation in the lower extremities was stopped by ligature of the abdominal aorta. Now these poisons by mere imbibition could enter the lymphatics as well as the blood-vessels, so that the absence of their usual effects in these cases must be attributed to a change effected by the lymphatics in the matters which they absorb.

Power by which the lymphatics and lacteals absorb.—I confess that the act of absorption in other parts, as well as in the intestines, is to me quite an enigma. Capillary attraction, by which some persons would explain so many processes in the animal body, accounts for the filling of capillary tubes only when they are empty, or when they have the power of emptying themselves from time to time; it does not explain the absorption and motion of the organic fluids. When, in the experiment before described, I witnessed the filling of the lacteals of the mesentery by milk, which was injected into the intestine so as to distend its coats, I fancied at the moment that I had discovered an explanation of the absorption of the chyle. But I gave up this idea at once when I recollected how slight the contractions observed in the intestines on opening the abdomen are, and that the small intestines generally appear collapsed. And I was still more induced to renounce this view on finding that generally, perhaps always, the injection of the lacteals in this experiment is attended with laceration of the internal coat of the intestines. Some kind of attraction must be exerted by the absorbents. As soon as the lacteals are filled beyond the point at which they pass through the muscular coat, the slightest contraction of the intestine by compressing the lacteals between the muscular fibres must tend to drive the chyle onwards, and the arrangement of the valves of the lacteals necessitates its flow towards the receptaculum chyli. When the contraction of the intestine ceases, a vacuum is produced in the lacteals which have been emptied, and their refilling is the necessary consequence. But although this may take place in the intestines, it can never occur in parts which possess no contractility; and in fishes the absorbents have no valves. It is probable, therefore, that some other kind of attraction, and this certainly not of a mere physical nature like capillary attraction, but an organic attraction of a kind hitherto unknown, is here in action. I have never seen the slightest motion in the villi of the intestines, although I have laid open the intestine in a living rabbit and examined its internal surface under warm water. Nor have I observed any sign of movement even in the lacteals of the mesentery, in the receptaculum chyli, or in the thoracic duct. I have applied the wires of a strong galvanic battery to the thoracic duct of a goat, which was opened as quickly as possible, while still alive, but

could perceive no contraction; it was not till sometime had elapsed that the duct appeared to have become somewhat narrower at the point to which the wires had been applied, and presented several very inconsiderable constrictions.

In no points perhaps do plants and animals so much resemble each other as in the ascent of fluids from absorbing surfaces in the absorbent vessels of animals, and the ascent of the sap in the vessels of plants. The ascent of the sap in plants is effected solely by the action of the roots and their spongiola.* The villi of the intestines are not essential organs for the absorption of the chyle; for the absorption by the lym-

* The absorption by the lymphatics in animals being involved in so much mystery, it appeared to me to be advisable to investigate the laws of the analogous process in plants.

It has been proved by Dutrochet, that the organs which effect the ascent of the sap in plants during the spring, are the terminal parts of the roots,—that the whole force by which the sap is impelled upwards is a *vis à tergo* exerted in the roots. Dutrochet cut off the end of the stem of a vine, which was about six feet high, and distinctly perceived that the cut surface of the stem continued to pour forth the sap uninterruptedly. The cause of the ascent of the sap, therefore, is not an attraction of the upper part of the plant for the sap in the lower part of the stem. Dutrochet then cut off the vine stem close to the ground, and observed that the effusion of sap from the upper extremity of the stem immediately ceased. The cause of its effusion, therefore, was not seated in the stem of the vine. The portion of the stem which still remained attached to the root, continued to pour out sap from its cut surface. Dutrochet now removed the earth from about the roots and divided them; the cut surface of the remaining portion of the roots still continued to emit sap. Continuing the excision of the roots lower and lower, he always observed, that the portion remaining in the ground still emitted sap, even until he reached the terminal parts of the roots. The terminal portions of the roots, therefore, being the seat of the constant absorption of the sap, must, by taking up successively fresh portions, necessitate the ascent of that already absorbed. Dutrochet placed one of the radicles, which terminate with a whitish cone, in water; and by the aid of a lens observed, that the cut surface became covered with water, which issued from the central part of the radicle.—(Dutrochet, l'agent immediat du mouvement vital. Paris, 1826, 90.) The absorption of matters by the mere extremities of the roots had been already demonstrated by De la Baisse and Hales. Hales immersed the extremity of the root of a tree in water, contained in a glass tube, and in six minutes observed a marked diminution in the quantity of the water. (Agardh, Algemeine Biologie der Pflanzen.)

The terminal parts of the roots are what Decandolle calls spongiola. Agardh remarks, that the structure of these parts does not differ from that of the rest of the roots, except that the cells are small, and therefore more numerous; but that the same cells which, when thus small and aggregated, have the power of absorption, in a short time attain their full developement, and cease to absorb, leaving this function to be performed by new cells which are formed after them and below them. Agardh attributes the ascent of the sap to a polarising action of the roots and leaves, by virtue of which the roots attract and the leaves exhale. This action he regards as something incapable of further explanation, like the polarising action of the magnet. This explanation cannot at any rate be applied to animals, for in them there is but one part of the act,—namely, the absorption by the radicles of the lymphatics, while, on the other hand, the lymph is poured into the blood.

phatics is performed in other parts without villi, and in the intestines of many animals there are no villi. Nevertheless, the villi of the intestines are in some measure analogous to the spongiola of the roots of plants; it must, however, be remembered that the absorbents in the villi have the same structure as in other parts which have no villi.

Dutrochet explained the phenomena of absorption both in plants and animals by the laws of endosmose. It is easy, however, to perceive that the phenomena of endosmose in dead animal membranes are by no means sufficient to account for the organic process of absorption in the animal and vegetable kingdoms.

If the lacteals in the intestine and mesentery be supposed to be filled with animal fluids, and chyme to be in contact with the villi or net-work of lacteals, the fluid parts of the chyme would, according to the laws of endosmosis, enter the lacteals; and the fluid, or dissolved parts of the matter already in the lacteals, would pass out and mix with the chyme; if the chyme were more fluid than the chyle in the lacteals—if the matters it held in solution were in a less concentrated state than in the chyle,—the chyme would enter the lacteals in larger proportion than the chyle would issue from them; if, on the other hand, the matter dissolved in the chyme were in a more concentrated state, the chyle would permeate the coats of the lacteals in an outward direction in larger quantity than the chyme would enter them. This, however, does not account for the wonderful process of absorption. If absorption is to be explained in a manner analogous to the laws of endosmose, it must be supposed that a chemical affinity, resulting from the vital process itself, is exerted between the chyme in the intestines and the chyle in the lacteals, by which the chyle is enabled to attract the chyme, without being itself attracted by it. But such an affinity or attraction would be of a vital nature, since it does not exist after death. To account for absorption, some might suppose that fluids are attracted by the external surface of the lymphatics, and repelled towards the cavity of the vessels by their internal surface; there are no facts either to confirm or to refute this hypothesis.

It is probable that there is no mechanical apparatus for absorption in the radicles of the absorbent system, since in plants no such apparatus exists.* Absorption seems to depend on an attraction, the nature of which is at present unknown, but of which the very counterpart, as it were, takes place in secretion; the fluids altered by the secreting action being repelled towards the free side only of the secreting membranes, and then pressed onwards by the successive portions of fluid secreted. In many organs,—for instance, in those invested with the mucous membranes,—absorption by the lymphatics and secretion by secreting organs are going on at the same time on the same surface.

* See note at preceding page.

Since the action of the absorbents depends on an organic property, circumstances which affect the organisation of a part will necessarily elevate or depress their action. Thus in inflammation, as Autenrieth remarked,* the action of the absorbents appears to be diminished, and hence the frequent occurrence of an enduring œdematous swelling around an inflamed part.

It is still uncertain how the remedial means, which are supposed to excite absorption, produce their effects; the cases, in which their action is evident, are few. There are substances called resolvents, which are capable of softening and dissolving the matters collected in superabundant quantity in the interstices of the elementary parts of tissues. The possibility of such a process taking place is shown apparently by the organic fluids themselves, in which one ingredient is frequently the menstruum for another; thus, for example, animal matters are kept in a state of complete solution by their organic union with mineral substances, as is the case in the serum, or with other organic substances, as in the bile, in which picromel is the solvent menstruum of the cholesterine. The use of resolvents in medicine is, however, very limited, because many substances, which out of the body have the power of dissolving animal matter, have a destructive action on living animal textures. The assertion, that the lymphatics continue to absorb after death, appears to me to be wholly without foundation.†

2. *Change effected by the lymphatic and lacteal vessels on their contents.*

The absorbent vessels, the parietes of which are supplied with capillaries, seem to effect a change in the composition of the chyle and lymph. The absorbent glands have the same action; they serve merely as means of increasing the surface of action; for, in the lower vertebrata, they are replaced by mere plexuses, and are, in fact, merely plexuses in a more highly developed form. The chyle in the lacteals of the mesentery, according to Tiedemann and Gmelin, is not coagulable until it has passed through the mesenteric glands. The lacteals and their glands appear, therefore, to have the power of converting, by the agency of their parietes, a part of the albumen of the chyle into fibrin. In many diseases this action of the lacteals on the elementary combination of their contents is modified, or the vessels themselves suffer from the action of fluids morbidly formed, as in scrofula.

The absorbents are endowed with a peculiar sensibility to the action of foreign matters, becoming painful, sometimes inflamed and swollen, so as to be distinguished through the skin by red streaks when such matters have been absorbed. Under the same circumstances, the glands in the neighbourhood of the absorbing spot swell and become also painful. Ordinarily, if the absorption of the irritating matter is not con-

* Physiologie, ii. 224.

† See E. H. Weber, loc. cit. vol. iii. p. 101.

tinued, the swelling disappears, but sometimes the glands inflame and suppurate. This enlargement of the neighbouring glands is observed to take place under various circumstances, such as the introduction of an animal poison under the epidermis, the application of a blister, the bite of a snake, a cut or prick received in opening a putrescent body, or the inunction of tartar emetic ointment or mercury; it often occurs, also, in glands near an inflamed part in which matter is forming. Thus the inguinal glands swell in cases of gonorrhœa, or of venereal infection of the genitals when there is no gonorrhœa. The mesenteric glands seem to stand in the same relation to the intestines as the superficial glands to the skin; they become inflamed when the intestines are inflamed and ulcerated, for example, in typhus abdominalis.

3. *The motion of the lymph and chyle.*

The powers by which the lymph and chyle are moved are unknown. It is possible that the absorbent vessels and thoracic duct propel their contents by imperceptible progressive contractions; but it is not known whether this is the case. Tiedemann and Gmelin could produce no contractions of the thoracic duct by the application of mechanical and chemical irritants, which Schreger had previously asserted that he had succeeded in doing. I applied the galvanic apparatus to the thoracic duct in a goat, but without producing any contractions; it was not till after some little time that some very slight constrictions of the duct were perceptible. Tiedemann and Gmelin, however, observed that the thoracic duct, when punctured, expels its contents in a jet. They suppose, therefore, that the lymphatics and lacteals, although not endued with rhythmic contractility, nevertheless have the power of propelling onwards their contents; an action which, if really exerted by them, must be facilitated by their valves; the arrangement of which, indeed, is such that even external pressure applied to the lymphatics or lacteals by the muscles, must have the effect of propelling onwards the lymph and chyle. The suction exerted by the heart on the venous blood during the dilatation of its cavities, must also have a similar influence on the motion of the chyle in the thoracic duct which communicates with the left subclavian vein; and this action of the heart may alone have the effect of causing the chyle to follow the motion of the venous blood towards the heart, while, from the presence of a valve at the point where the thoracic duct opens into the vein, no venous blood can be forced back into the thoracic duct by the impulse arising from the heart's contraction. The sucking action of the heart, however, is not the primary cause of the motion of the chyle; for Autenrieth,* Tiedemann, and Carus† have observed that when a ligature is applied to the thoracic duct, the part of the duct below the ligature becomes distended even to bursting.

* Physiologie, ii. 115.

† Meckel's Archiv. iv. 420.

The motion of the lymph and chyle depends most probably, therefore, principally on the continued absorption going on in the radicle net-work of the lymphatics, in the same way as the ascent of the sap in plants, during the spring, depends solely on the constant absorbing action of the roots.

The lymphatic hearts which I have discovered in reptiles must considerably facilitate the motion of the lymph in these animals. These hearts discharge the lymph of the lower part of the body directly into the ischiadic vein, that of the upper part of the body into a branch of the jugular vein. In mammalia and man it is only in the subclavian veins that the chyle and lymph are mixed with the blood, all the chyle and the greater part of the lymph being poured into the left subclavian vein by the thoracic duct. The lymph and chyle are often still detectible in the blood of the superior cava. The process of their conversion into blood in their course through the circulation has already been described at page 145. I have never been able to perceive the slightest motion in the thoracic duct and receptaculum chyli, or in any part of the absorbent system of mammalia; and in reptiles the lymphatic hearts are the only parts of the absorbent system in which I have perceived any contractions.

The rate of the motion of the lymph and chyle is quite unknown. It appears to be much slower than that of the blood, and is much less rapid than Cruikshank and Autenrieth supposed. Some idea of the rate at which the chyle moves may be formed by observing the time required for the distended lacteals in the mesentery of an animal just opened to become invisible, and by ascertaining the quantity of the fluid which can be collected from the thoracic duct. In Magendie's experiment half an ounce of chyle was collected, in five minutes, from the thoracic duct of a middle-sized dog. Collard de Martigny obtained nine grains of lymph, in ten minutes, from the thoracic duct of a rabbit which had taken no food for twenty-four hours. Collard de Martigny having pressed out the lymph from the principal lymphatic trunk of the neck in a dog, the vessel filled again in seven minutes; in a second experiment it filled in eight minutes.*

In the case already related, in which lymph escaped from a wound on the foot of a young man, the lymphatics on the dorsum of the foot and great toe became sufficiently filled in a quarter or half an hour to enable us to collect from them a considerable quantity of lymph in a watch-glass. In frogs the quantity of the lymph, and the volume of the cavities in which it is contained, are very great. If the capacity of each of their lymphatic hearts, of which the posterior are the larger, is estimated at one cubic line, the quantity of lymph which they would project into the veins in a minute, supposing that they emptied themselves

* Journ. de Physiol. t. viii.

entirely at each contraction, would be $4 \times 60 = 240$ cubic lines, since they contract about sixty times in a minute. But they expel only a part of their contents at each contraction.

[Prof. E. H. Weber* has described a *visible circulation of the lymph.* It has been several times observed that the capillary blood-vessels, when viewed by the microscope, appear broader than the stream of blood in them. M. Poiseuille,† while watching the circulation in the capillaries, perceived that occasionally a globule of blood is thrown into the transparent space at the side of the current, and immediately loses its rapid motion; that it becomes quite stationary for a time if wholly without the current, while if only partially immersed in the transparent space, it is rolled along, as it were, by the blood moving rapidly over it. M. Poiseuille inferred from these observations, that there is, in contact with the parietes of the vessels, a layer of liquor sanguinis which does not move; and he states that M. Girard has demonstrated, that in the case of inert tubes of small diameter, the portion of a fluid moving through them which is in contact with their parietes is stationary. The appearances above described have been observed by Prof. Weber, and attributed by him, but less correctly, to the motion of lymph-globules in lymphatics surrounding the blood-vessels. The bodies which move thus slowly and irregularly along the sides of the current of blood are, for the most part at least, globular, as he states, but they appear to be larger than lymph-globules, and are certainly within the blood-vessels—they are evidently moved, as Poiseuille describes, by the same force that moves the current of blood, and are occasionally seen to re-enter this current.]

* Müller's Archiv. 1837. Heft ii.

† Ann. des Scienc. Nat. Fevr. 1836, t. v. p. 111.

SPECIAL PHYSIOLOGY.

BOOK THE SECOND.

Of the Chemical Changes produced in the Organic Fluids and Organised Textures under the influence of the Vital laws.

The power by which elementary substances are, in the organic system, united into ternary and quaternary compounds, in opposition to their affinities, which would, under other circumstances, lead them to unite to form binary compounds, is without doubt a peculiar "force" or "imponderable matter" unknown in inorganic nature. This force or principle is probably the same that governs the formation and nutrition of the different organs of the body after a plan of strict adaptation.* To attribute to electricity the production of all organic compounds would be a perfectly gratuitous hypothesis. Until the properties of the principle which influences organic combinations are known, it can be spoken of merely as something, the existence of which is certain, but of which the nature cannot be defined,—the vital principle or organising force. The law which regulates the action of parts endowed with this power on other substances is that of assimilation.

The material changes which occur in the organic system may be divided into the purely chemical and the organic chemical.

1. Purely chemical changes, regulated by the laws of elective affinity, ensue in the animal system when the vital principle loses its influence on the textures of the body, or becomes incapable of counterbalancing the power of chemical affinity.

Concentrated acids and alkalies unite with the component elements of living animal bodies, and produce new substances, the animal matter being destroyed. Dilute muriatic and acetic acids in the gastric juice serve for the solution of alimentary substances. Berthollet supposes that the action of the caustic metallic oxides and salts depends on their yielding oxygen to the animal matter. When muriate of antimony is used, the inorganic substance is reduced, and the organic body oxidised. Bichloride of mercury is converted into the chloride by several organic substances.

* See pages 22—28.

These purely chemical actions are of frequent application in therapeutics. The property which albumen possesses of precipitating corrosive sublimate, and uniting with it to form an insoluble substance, suggested to Orfila the happy idea of trying it as an antidote.* An antidote, as Huenefeld remarks, must have a strong affinity for the poison, and but slight chemical affinity for the animal body, so that it may be introduced into the system without ill effects. Sulphur neutralises arsenic, and, by giving rise to an insoluble compound, renders it less hurtful. It is on account of their insolubility that preparations of mercury which contain sulphur are inert in the treatment of syphilis.† The soluble sulphates are antidotes for poisoning by barytes and salts of lead, because the sulphates of barytes and of lead which are formed are insoluble.‡ Magnesia neutralises the acid of the stomach. The success attending the administration of carbonates of alkalies in cases of lithic acid deposit, and of formation of calculus, from the urine, depends on the lithic acid being dissolved by the alkalies, and the urine rendered alkaline. Salts of vegetable acids are useful in the same way, being converted into carbonates in the animal body or yielded in that form to the urine. Nitric acid, chlorine, and chlorates have been applied to sores of hospital gangrene and to cancerous sores, with success, in preventing the developement of sulphuretted hydrogen, ammonia, and hydrosulphate of ammonia from them. The use of mineral acids in putrid fever with a tendency to alkalinity of the fluids may be regarded in the same light.§

The colouring matter of madder evinces a strong affinity for phosphate of lime even in the living body, the bones being the only parts which are coloured by it when it is taken with the food. Lastly, many foreign substances taken up into the circulation, undergo change in part, and are again expelled from the system in their changed or unchanged state.

2. In other cases certain substances, particularly those generated by the decomposition of the organic matter in diseased animals, act on other living animals in a manner which resembles the chemical process of fermentation. Thus, contagions give rise to the production of similar changes of composition in the animal matters of other living beings.

3. Chemical compounds and simple elementary substances may, however, by affording the components which were deficient for the formation of new organic compounds in the body, favour the production of these compounds instead of decomposing them, and thus assist the operations of the vital principle. Thus the admixture of a certain proportion of mineral substances in the food is necessary. The change effected in the blood during respiration is an organic chemical change, in which a binary compound is formed and separated from the blood.

4. Organic substances again may reciprocally decompose each other

* Huenefeld, Physiol. Chemie, i. pp. 65. 89. † Ibid. p. 66.
‡ Ibid. p. 67. § Ibid. p. 72.

even without the influence of the vital principle. Thus saliva, according to Leuchs,* converts boiled starch into sugar, and Tiedemann and Gmelin have shown that starch is changed in the stomach of animals into gum of starch and sugar. Fibrin or muscle are stated, like yeast, to excite fermentation in solution of sugar. Dr. J. Davy, however, on performing the experiment with beef, and continuing it three or four days, obtained no alcohol, but in its place gum.† Certain organic fluids, such as saliva, gastric juice, bile, and pancreatic juice, serve to effect similar chemical changes in the animal economy. It is true that both the substances which act on each other in this way are quaternary compounds, and the products may still be quaternary compounds, without being reduced to binary combination. But organic substances once formed, even when subjected to the action of inorganic compounds out of the body, frequently undergo merely a change of organic combination. In the animal system, however, the action of organic fluids on one another is modified by the vital principle. The action of saliva and of bile in the process of digestion is not intelligible from the effects which they produce on organic compounds out of the body.

5. The organic assimilation is, in the first place, evidenced in the changes of composition which organic fluids undergo while exposed to the influence of living surfaces endued with the vital principle. Thus, the composition of the chyle absorbed from the alimentary canal undergoes a change in the lacteal system; the quantity of fibrin that it contains being greater in proportion to the number of mesenteric glands through which it has passed. In the formation of the different secretions the same action of the tissues on the fluids exists, but in a modified form, inasmuch as the components of the blood, which have been changed by the action of the tissues, are in this case separated from it.

6. Lastly, assimilation is still more remarkably manifested in the conversion of the organic fluids into formative particles of the organs in the process of nutrition. The blood in the capillaries comes in contact with the smaller particles of nerves, muscles, mucous membrane, glands, &c. and each tissue exerts its assimilating action on the substances contained in the blood, changing their elementary composition, nourishing itself by their appropriation, and at the same time imparting to them the property of organising other matters in their turn. The essential phenomenon of this kind of assimilation is seen in the germinal disk (blastoderma) of the egg before vessels and the blood are formed. The germinal disk increases at the edges so as to form the germinal membrane at the expense of the yolk. The albumen of the yolk gradually undergoes a change of composition, and at last ceases to be coagulable by heat. As soon as vessels are developed, growth is effected by the enlargement of the particles between the capillaries, and by the formation of new vessels. If in an organised texture, or living substance, A, B, C, and D are the elements

* Poggendorf's Annal. 1831. 5. † Kastner's Archiv. 1831. 396.

which are combined in certain proportions to form each organic molecule, the organising principle of the part effects not only the combination of A, B, C, and D to form component particles, but also the union of these particles to form organic tissues; and the organic fluids in contact with them are compelled, as it were, to change their composition to the combination of A, B, C, and D, that is, to form atoms of this composition, and to unite these atoms with the assimilating organ. By atoms here are intended not organic globules, but those invisible atoms which are supposed, in the chemical theory, to constitute the ultimate particles of a compound.

The production of vital phenomena—of muscular contraction, &c.—is constantly giving rise to the decomposition of a certain quantity of organic material, to replace which new matter is supplied by the nutriment. In this respect, however inapt the comparison may be in other points, the animal machine resembles every other machine the action of which necessitates the destruction of some material, and which, like the steam-engine, requires a certain quantity of new matter for the continuance of its action. The most wonderful part of the process is, that, while the system gets rid of its old material and developes vitality in the new, it does not lose any vital power with the matter which it casts off; it would, therefore, almost appear, either that the vital principle leaves the decomposed elements, and unites itself to the new matter, or that the nutriment itself is a source of increase of the vital principle, supposing that a portion of this principle becomes inert with the destruction of the old components of the animal body.*

The first general law that regulates the formation of different animal substances seems, as Autenrieth remarks, to be the law of the attraction of similar parts for each other. But the particles of living structures have a great attraction among themselves, and therefore do not leave their combination to unite with the particles of the nutrient fluid; they attract to themselves, however, the analogous particles from the blood; so that in the exertion of this affinity it seems to be the blood which principally suffers a separation of its elements. I cannot conclude these remarks better than in the words of Autenrieth:—"Bone secretes only osseous matter; muscle secretes fibrin, and even a morbid scirrhus or a steatoma grows by the deposition of analogous matter. The growth, by the attraction of similar particles, is not manifested merely in the chemical components of an organ; even in its organisation a similar law prevails. A polypous excrescence of the vagina or nostrils differs less in chemical composition than in its organisation from the surrounding healthy parts. Once formed, however, it continues to a certain extent to grow with its own peculiar structure. A cicatrix, although it possesses a structure different from the original organisation of the skin, continues to be nourished in the same form; it even enlarges as the rest of the body grows."†

* See page 39.

† Autenrieth, Physiol. ii. p. 181.

SECTION I.

Of Respiration.

CHAPTER I.

Of Respiration in general.

Composition of the atmosphere.—The essential respirable component of the atmosphere is the oxygen, which constitutes twenty-one parts in 100, seventy-nine parts being nitrogen. The proportion of carbonic acid in the atmosphere is extremely small; 10,000 volumes of atmospheric air contain, according to M. de Saussure, only 4·15 of carbonic acid. In the open country the maximum proportion of this gas was 5·74, the minimum 3·15, in 10,000 parts. In the town of Geneva the air contained 0·31 more carbonic acid than in the country.* There are also local impurities, such as an organic matter, which rain water likewise contains, and which, with the concurrent action of light, reddens solution of silver.† Air, in which men or animals are breathing, loses a certain proportion of its oxygen, and in its place acquires nearly the same volume of carbonic acid. The same change is effected by respiration in pure oxygen. Although we do not regard respiration really as a species of combustion, yet the great similarity of the changes produced in the air by the two processes cannot but be remarked. In respiration, as in combustion, the nitrogen seems to act quite a neuter part, merely moderating the process by diluting the oxygen.

Respirable and irrespirable gases.—In considering the various gases in reference to respiration and the respiratory organs, a distinction must be made between those that are merely incapable of supporting the process, and those that are actually poisonous in their action. Nitrogen and hydrogen are instances of the former kind; they do not support life when respired in their pure state, but when mixed with the necessary quantity of oxygen they are perfectly innoxious. Those gases, which from their affinity for animal matters are decidedly noxious to the system, must be again divided into two classes; for several gases can be taken into the lungs although poisonous in their action, while others cannot be inspired in any considerable quantity, on account of their exciting spasm of the respiratory organs, particularly of the glottis.

The gases may be classed according to their physiological effects as follows:—

* Berzelius, Jahrb. übersetzt. v. Woehler, xi. 64.

† Gmelin's Chemie, i. 442.

I. *Those which support the chemical process of respiration.*

a. Permanently without injury to life.—Atmospheric air.

b. For a certain period, but not permanently.—Oxygen and nitrous oxide. The respiration of oxygen causes, it is said, even the blood in the veins to become of a bright red colour. But at length its effects are injurious. Allen and Pepys, however, experienced no ill effects from respiring pure oxygen; and a pigeon which they placed in oxygen gas merely became restless and embarrassed, but recovered when restored to the air. Lavoisier and Seguin perceived no disturbance of the functions in Guinea pigs which were kept twenty-four hours in oxygen gas. Allen and Pepys found that when oxygen was inhaled, a larger proportion of carbonic acid was contained in the gas expired than under ordinary circumstances; but in the case of a pigeon, less carbonic acid seemed to be formed than during respiration in atmospheric air. The respiration of pure oxygen is injurious to phthisical patients. Nitrous oxide gas supports life for a short time, but soon has a stupifying and intoxicating effect, producing excitement, illusions of the senses, confusion of mind, and, at length, syncope.* A portion of the gas is absorbed into the blood, which becomes of a purple colour, while the face and lips have the colour of death. Nitrogen and a scarcely perceptible quantity of carbonic acid are expired with the gas from the lungs.

II. *Gases which are respirable, but do not support the chemical process of respiration.*

a. Gases which have no positive injurious influence, but fail to support life, simply from containing no oxygen.—Nitrogen and hydrogen. Lavoisier and Seguin caused Guinea pigs to respire a mixture of equal proportions of oxygen and hydrogen; no particular symptoms were produced, and the experimenters found that the same quantity of oxygen was consumed as when the mixture consisted of equal quantities of oxygen and nitrogen, and that no hydrogen was absorbed. The researches of Allen and Pepys seem to show that when hydrogen alone is respired, nitrogen is exhaled from the blood. Allen and Pepys and Wetterstedt† state that the respiration of hydrogen produces a tendency to sleep. I placed some frogs in impure hydrogen, as prepared from zinc and dilute sulphuric acid, and they became insensible in a few hours; but when I had previously purified the hydrogen and freed it from the fœtid oil, by passing it through alcohol, a frog lived in it twelve hours, breathing from time to time; at the end of twenty-two hours it was apparently dead, but still moved slightly when it was taken out and

* Sir H. Davy, Researches on Nitrous Oxide.

† Berzelius, Thierchemie, 101. Traité de Chemie, traduit par Esslinger, t. vii. p. 106.

pinched. In subsequent experiments frogs lived only three or four hours even in pure hydrogen.

b. Poisonous gases.—Carburetted hydrogen, phosphoretted hydrogen, sulphuretted hydrogen, arseniuretted hydrogen, carbonic oxide, cyanogen (?). Atmospheric air which contains $\frac{1}{1500}$th of its volume of sulphuretted hydrogen will, according to Thenard, destroy a bird; when it contains $\frac{1}{800}$th of its volume, it will destroy a dog; and with $\frac{1}{250}$th, a horse. The above gases also destroy life when injected in small quantities into the blood.*

c. Gases which in large quantity cannot be inspired, on account of their producing spasmodic contraction of the glottis, and which, when inspired in small quantities, excite coughing.—All acid gases, as well as carbonic acid gas, chlorine, nitric oxide, fluoboric acid gas, fluosilicic acid gas, and ammonia. Atmospheric air which contains more than 10 per cent. carbonic acid quickly produces asphyxia. Any fluid, water for instance, acts on the glottis like a solid body, exciting it to spasmodic contraction, so as even to produce suffocation; but very little irritation is produced by the presence of fluid in the lungs themselves, and a considerable quantity of fluid is borne, when injected into them by an opening in the trachea. In the first case, death is produced by the closure of the glottis, which is unattended by ill consequences if there is an opening in the trachea.

Aquatic respiration.—A part of the animals which inhabit the water —the reptiles and aquatic mammalia, namely,—come to the surface to respire atmospheric air, and breathe by means of lungs; others, as the fishes, have gills, and respire the water itself, or rather the air which the water contains. The water of lakes, rivers, and the ocean, is impregnated with atmospheric air, or, more correctly, with oxygen and nitrogen, in determinate proportions, which it absorbs from the atmosphere. Humboldt and Provençal obtained from 10,000 parts of Seine water, by boiling, from 264 to 287 parts of gas, of which from $\frac{306}{1000}$ to $\frac{314}{1000}$ was oxygen, and from $\frac{6}{100}$ to $\frac{11}{100}$ carbonic acid. It must not be imagined that the water itself undergoes any change during respiration, it is the gas with which it is impregnated that alone is changed, the oxygen being removed and the carbonic acid increased in quantity. When fishes are made to respire water impregnated with oxygen and hydrogen, the oxygen only is absorbed, the quantity of the hydrogen remains unchanged. If fishes are placed in water which has been subjected to long continued boiling, they die from want of oxygen in the space of four hours, during which time their respiratory movements are continued. Priestley found by experiment that fishes will live ten or fifteen minutes in water which had been freed from air and afterwards impregnated with nitric oxide, but that as soon as the smallest

* Nysten. See page 142.

quantity of atmospheric air gained access to such water, the fishes were seized with convulsive motions and died.

The respiratory movements.—The chemical process of respiration is not essentially dependent on the respiratory movements. They merely serve to expel the air or water which have undergone the change induced by the chemical process that is constantly carried on between these media and the blood, and to renew the supply of fresh air or water.

The lungs, by their internal surface, offer an immense expansion for the action of the blood and air on each other; and, as they are never completely emptied by the act of expiration, this action is constant. By the contraction and dilatation of the chest, the motion of which the lungs follow, a portion of the altered contents of the pulmonary reservoir is first expelled, and then a new supply introduced, to undergo change in its turn. The fishes take in the fresh water by the mouth, and then expel a portion, passing it through the branchiæ, the opercula or gill-covers being alternately opened and closed.

Volume of air respired.—Sir Humphrey Davy calculates that the human lung, after the strongest expiration, still contains thirty-five cubic inches of air, and after an ordinary expiration, 108 cubic inches; he regards from ten to thirteen cubic inches as the quantity usually expelled at each expiration.* Herbst † found that adults of large stature, when breathing tranquilly, inspire and expire from twenty to twenty-five cubic inches; persons of smaller stature sixteen or eighteen cubic inches.

Necessity of respiration.—The length of time during which life can be supported without respiration being performed varies very much in different animals, being shorter in the vertebrata, and more especially in the warm-blooded vertebrata than in other animals. Warm-blooded animals, placed in the vacuum of the air-pump, die in less than a minute; birds, even in from thirty to forty seconds. Reptiles will live a considerable time in a vacuum, and in irrespirable gases; and in Carradori's ‡ experiments a tortoise placed under oil lived from twenty-four to thirty-six hours. Frogs die in less than an hour, when placed under oil; in water impregnated with air they live a long time, respiration being carried on by the skin. Edwards says that toads, which he confined in baskets and placed in the Seine, lived several days; and Spallanzani and Edwards § have found them live a few hours even in water deprived of its air. I have wholly removed the lungs of frogs, after tying them at their root, and the ani-

* [The numbers quoted by the author, although mentioned by Sir H. Davy, in his different experiments, are not those which he considered most accurately to indicate the capacity of his lungs. Those which he gives are 254 cubic inches in a state of voluntary inspiration; 135 in a state of natural inspiration; 118 after a natural expiration, and 41 after a forced expiration. This capacity Sir H. Davy considered below the medium, his chest being narrow.]

† Meckel's Archiv. 1828.

‡ Ann. de Chim. et d. Phys. v. p. 94.

* Meckel's Archiv. v. 141. Influence of Phys. Agent. on Life, p. 31.

mals still lived about thirty hours, respiration being performed most probably by means of the skin. In the experiment mentioned above, the frog placed in pure hydrogen showed distinct signs of life at the end of twelve hours, and respired from time to time, and after twenty-two hours was still only in a state of asphyxia. In experiments instituted by Humboldt and Provençal, gold fishes lived an hour and forty minutes in water deprived of its air by long boiling; in water impregnated with carbonic acid, and in carbonic acid gas, on the contrary, fishes died in a few minutes; while in nitrogen and hydrogen, in which fishes keep their gill-covers closed, they lived five hours.

The lower animals differ very much in the degree in which respiration is necessary to them, but, generally speaking, it appears that respiration is not essential for the maintenance of their life. Carradori states that insects die immediately when immersed in oil, and according to Treviranus they may be killed very quickly by merely smearing the openings of the respiratory organs with oil. Biot, however, found insects of the families blaps and tembrio live eight days under the air-pump in air rarefied to a tension of from one to two millimeters. The larvæ of the gad-fly, in Schroeder Van der Kolk's experiments, lived a considerable time in irrespirable gases. The larvæ of some insects live in putrefying vegetable and animal substances, and seem to have little need of pure oxygen, although no insect is known which has not a system of tracheal tubes, and which, therefore, during life respires air. Berzelius saw larvæ living in spring-water which contained carbonate of iron and some sulphuretted hydrogen. Leeches seem to live a long time without fresh water; while Tiedemann found that holothuriæ die in a single day if the sea-water in which they are kept is not renewed. Intestinal worms, which inhabit other living beings, seem to dispense with respiration.*

* For an account of the respiration of hybernating animals refer to page 77. The respiration of ova will be treated of in the third chapter of this section. The best works of reference on the subject of respiration in general, are—Goodwyn on the Connexion of Life with Respiration, London, 1788. Lavoisier and Seguin, Ann. d. Chim. 91, 318. Menzie's Tentamen Physiol. de Respirat. Edinb. 1790. Crell, Ann. 1794, ii. 33. Sir H. Davy, [Researches on Nitrous Oxide.] Gilbert's Ann. 19. 298. Pfaff, in Gehlen J. de Chem. v. 103. Provençal et Humboldt, Schweigger's Journ. i. 86. [Mém. d'Arcueil, t. ii.] Edwards, Ann. de Chim. et de Phys. 22. 35, [and Influence of Physical Agents, &c.] Dulong, Schweigger's J. 38. 505. Despretz, Ann. de Chim. et de Phys. 26. 337. Spallanzani, Mém. sur la Respiration, Genève, 1803. Hausmann, de Anim. Exsang. Resp. Hannover, 1803. Sorg, de Resp. Insect. et Verm. Rudolstadt, 1805. Nitzsch, de Resp. Anim. Viteb. 1808. Nasse, Meck. Arch. ii. 195. 435. Treviranus, Zeitschr. für Physiol. iv. 1.

CHAPTER II.

Of the Respiratory Apparatus generally.

Many of the lower animals appear to respire by their entire surface. When a determinate portion of the external membrane destined to effect certain changes in the air, or in the water impregnated with air, which comes in contact with it, is developed in a small space into a great extent of surface, so as to render the contact with this air or water more extended, it constitutes a respiratory organ.

Different forms of the respiratory organ.—The developement of the respiring surface may take place either towards the interior of the body in the form of ramified or sacculated cavities called lungs, (figs. 20, 23, and 24,) or towards the exterior in the form of lamellated, ramified, pectinated, tufted, ciliated, or pinnated processes, called branchiæ, (figs. 3, 4, 8, and 19,) in which nature seems to have exhausted all imaginable variations of form in the increase of surface towards the exterior. In the third form of respiratory organ, the increase of the surface for the contact of the air and the animal textures is obtained by the developement of a system of tracheal tubes, ramified to extreme fineness, and spread through the smallest portions of all organs of the body (fig. 22). This is the tracheal system of insects, and the tracheary arachnida. The lungs generally respire air; there are, however, exceptions to this; for instance, the respiratory organ of the holothuria consists of a tube ramified in an arborescent form, (fig. 18,) in which the respiratory function is performed by water being taken into the tubes, and again expelled from time to time. In animals provided with branchiæ or gills, the respiration is generally effected by means of water, but sometimes by air, as is the case in the terrestrial crustacea.

Lungs and branchiæ, in their extreme forms, are completely distinct, but they often approach each other in their essential characters so nearly that it is difficult to determine to which type they belong. Thus, the gills of the cyclostomata, and of the sharks and rays, are inclosed in sac-like cavities, and the branchiæ of the asidia form a branchial sac; but the characters of the two kinds of organs are still more confounded together in the pulmonary arachnida, in which the respiratory organs have the characters both of lungs and branchiæ at the same time (fig. 21); and when Treviranus called them branchiæ, and I named them lungs, we were perhaps both equally correct or incorrect. In some insects, too, there is a mixed form of respiratory organ, partly branchial partly tracheal.

In the infusoria the only respiratory organs seem to be delicate cilia, with which, in many species, the surface is in part or wholly occupied; they are so minute that it requires the highest magnifying powers to see them. *In the polypifera* the whole surface seems to serve the function

of respiration. In some, as the alcyonella, the tentacula seem to be at the same time branchiæ.

Fig. 18.†

Among *the echinodermata* the respiratory organ of the holothuria is remarkable; it is a tube ramified in an arborescent form with terminal cellules, (fig. 18,) respiration being performed by the contact of water taken in by the trunk with the inner surface of the organ. In the asterias family the respiratory organs are, according to Tiedemann, soft tubes upon the skin of the animal, into which the water has access.*

In the annelida the respiratory organs are sometimes tufted branchiæ of a branched form, (fig.19,) as in the arenicola, and similar organs on the feet of the nereides. Sometimes respiratory sacs exist, which lie concealed under the skin, each having a separate external opening, as in the lumbrici, naides, and hirudines; I have however, in one case observed that the peculiar respiratory sacs of the officinal leech contained a fluid secretion,—a small quantity of whitish matter.

Fig. 19.‡

Among the *mollusca* some breathe in the water by means of branchiæ, others by lungs in the air. The first mode of respiration is that of the cephalopoda, (fig. 4,) some of the gasteropoda, and the conchifera (fig. 3); the second is the mode of respiration of another part of the gasteropoda, as, for instance, the helicina and limacinæ (fig. 20). The branchiæ are in the form of plicæ, or laminæ, which are united parallel

* Tiedemann, Anatomie d. Röhrenholothurie, &c.

† [The holothuria, after Tiedemann.—1. The respiratory organ communicating with the cloaca (2); 3. the mouth; 4. tentacula; 5. contractile sac connected with the system of water tubes; 6. organs of generation; 7. the intestine.]

‡ [The half of a single segment of the amphinoma, showing—1. the tufted ramified branchia: 2. the dorsal oar; 3. the ventral oar; 4. membranous appendages of the fleshy tubercles, or feet, which support the bristles (5). Copied from the Cyclopædia of Anatomy.]

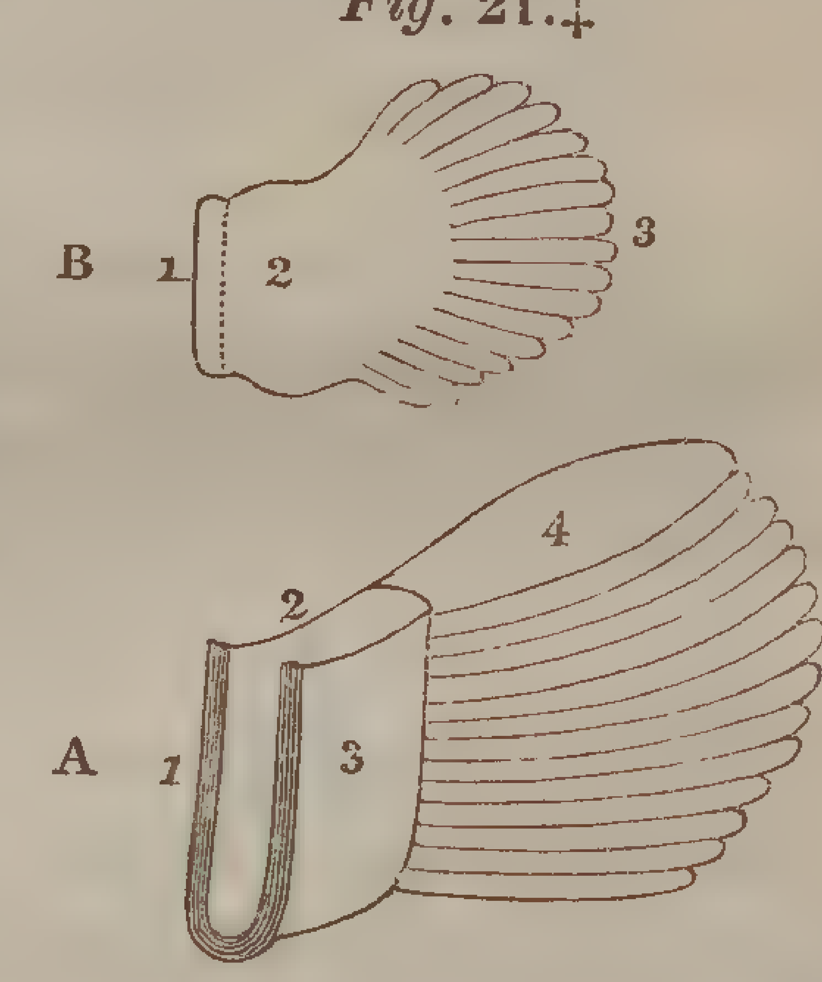
to each other, or arise from one shaft, as in the sepia (fig. 4); or they are ramified, as in the doris, in which they surround the anus. In the conchifera there are on each side, running the whole length of the animal, two leaf-like branchiæ (17.17, fig. 3), each consisting of two layers, between which the ova find their way, to be there developed.* In the ascidiæ the branchiæ form a sac-like vestibule from which the alimentary canal commences, the inner membrane of the sac forming pectinated processes. The pulmonary gasteropoda are partly aquatic, as, for instance, the fresh-water snails, the limnæa, &c. and these come to the surface to take a supply of air; others are terrestrial, as the limax and helix. The respiratory organ is a pulmonary sac, the external mouth of which opens and closes regularly (fig. 20).

Fig. 20.†

In *the crustacea* the organs of respiration are branchiæ, and this function is, in nearly the entire class, performed in the water. In the decapoda the branchiæ are enclosed in a separate cavity at the side of the thorax, and consist of a number of branchial pyramids. In the brachyurous decapoda, each of the pyramids is formed of lamellæ united to the axis of the pyramid in a pinnate form, but in the macrourous decapoda the lamellæ are replaced by filaments. In the aquatic aselli the branchiæ are simple lamellæ; in the terrestrial aselli, which respire air, they are simple hollow leaf-like appendages. In several of the crustacea the branchiæ are more vesicular in form, as in the amphipoda. The branchiæ of the crustacea are attached either to the feet or to the abdominal surface of the body.

The arachnida are divided into the pulmonary and the tracheary arachnida. The respiratory organs of the first order are situated at the under surface of the abdomen. They are small sacs opening externally, each by a separate stigma. The interior of the sac is divided in several compartments by parallel partitions or lamellæ (fig. 21 A); and when the sac is inflated from the external stigma, the compartments between the partitions become protruded externally, so

Fig. 21.‡



* Von Baer, Meckel's Archiv. 1830.

† [The limax or common snail.—1. The pulmonary sac; 2. the opening by which the air enters; 3. the veins which collect the blood from the body, and afterwards form a net-work over the pulmonary sac; 4. the auricle of the heart, which receives the aerated blood by numerous orifices; 5. the ventricle giving off two great systemic arteries.]

‡ [Pulmonary sac of the scorpion, from the original figures of Professor Müller, in

that the surface of the sac presents the same series of divisions as exists in the interior (fig. 21, B). In most of the arachnida there is but one pair of sacs; in others, as the mygales, two pair; and in the scorpionidæ there are four pair.* The aquatic arachnida respire the air which is confined among the hairs of their body when they descend into the water. The hydrachnida and pycnogonida would seem not to respire air at all. The tracheary arachnida, as the solpuga, chelifer, phalangium, and acarides, resemble the insects in the structure of the tracheal tubes, which ramify through all parts of their body. Dugès has also observed arachnida,—the dysdera and segestria,—which have, at the same time, both pulmonary sacs and tracheæ. The posterior two of the four stigmata of these arachnida belong to the tracheæ.

Fig. 22.‡

All insects have a system of ramifying tracheæ, and in the greater number the respiration is aërial, the air being inhaled through a number of stigmata, which are generally situated at the sides of the rings of the abdomen.† Through the stigmata the air is carried by the tracheæ, in some insects, into vesicles from which the rest of the tracheal tubes arise; in others, into longitudinal trunks, which ramify throughout the most delicate parts of the animal (fig. 22).§

Meckel's Archiv. 1828.—A. Portion of sac enlarged; 1. border of the stigma; 2. internal wall of the sac; 3. external wall of the sac; 4. one of the septa; B. sac inflated; 1. margin of the stigma; 2. undivided part of the sac; 3. divided portion of the sac inflated.]

* I have described the pulmonary sacs of the arachnida more fully in Meckel's Archiv. 1828, and in the Isis, 1828.

† See the representations of the tracheal system of many insects by Marcel de Serres, Isis, 1819, iv.

‡ [Principal tracheæ of the mantis religiosa, seen from the abdominal surface, after Marcel de Serres, loc. cit.—1. Communications of the tracheæ with the stigmata; 2. tracheæ to the palpi, mandibles, &c.; 3. nerves of the antennæ; 4. tracheæ of the legs; 5. ditto of the thorax; 6. ditto of the abdomen.]

§ In several insects, particularly in the orthoptera, there are distinct respiratory movements—alternate dilatation and contraction of the abdomen. Beetles, before

The larvæ of many insects breathe by means of branchiæ in the water; and some insects, which in the larval state are aquatic, likewise respire water when they have attained their perfect condition, although they have an internal tracheal apparatus. In place of stigmata, these insects have branchiæ at the commencement of the tracheæ. These branchiæ have the power of separating from the water the air which it contains, and which then passes into the ramified tracheæ in the gaseous state. Branchiæ are most frequent in the larvæ of the neuroptera.*

flying, seem to inflate themselves with air so as to unfold their wings, which, like other parts of the body, are supplied with air tubes. Treviranus has recently asserted that the stigmata of some insects are quite imperforate; but Burmeister has already refuted this assertion.—(Burmeister, Entomologie, Berlin, 1832, p. 172; to which I refer for a description of the stigmata.) Some insects live in the water, but come to the surface to inhale air; such is the case with the larvæ of many dipterous insects,—the hydrocoris or water-bug, and some aquatic coleoptera. The dytiscus comes to the surface and inhales air by the stigmata near the anus. The hydrophilus carries with it into the water bubbles of air entangled among the hairs of its body. Both these insects, while larvæ, have their stigmata at the caudal extremity. The larvæ of the common gnat—culex pipiens—has one trachea opening in the last abdominal ring, while the pupa has two projecting out of the thorax. Other species allied to this gnat have branchiæ, and respire water while in a state of larva. But the larva of the chironomus again has two tracheæ at the caudal ring. In the stratiomys, the last abdominal ring ends in an air tube. The air tube of the larvæ of the eristalis, which lives in the filth of sloughs, sewers, and privies, is very interesting. The last ring of the body is elongated into a membranous tube, within which there is a second horny tube; and this, like the trachea of the gnat and stratiomys, is provided with a circle of bristles for the purpose of suspension on the surface of the water. The larva extends the tube to the surface of the water, the inner portion of the tube being protruded when necessary, so that the tube can thus be elongated to an extraordinary extent. The larva is, by this apparatus, enabled to live at the bottom of the fluid while it respires at the surface.—(See Burmeister, l. c.) Some water-bugs also, the nepæ and ranatræ, have tracheæ.

* The branchiæ are, in some insects, hair-like filaments which contain in their interior the commencement of the tracheal tubes. The filaments are sometimes united in a radiated form, or they are branched. Such are the branchiæ of the larvæ and pupæ of several gnats. The branchiæ in several neuropterous insects are in the form of lamellæ. The larvæ of the gyrinus respire by means of hair-like branchiæ at the sides of the rings of the body. Branchiæ are most frequent in the larva of the neuroptera. The ephemera has, at the sides of the body, fin-like branchial lamellæ, in the interior of which the air tubes take their rise. The branchiæ of the larva of the dragon-fly are situated in the last ring of the body. In the agrion they consist of three great fringed lamellæ. The tuft-like branchiæ of the larvæ of the libellulæ are situated in the rectum, so that the tufted ends of the stems of the air tubes penetrating the membrane of the intestine project into its cavity. The larvæ of the phryganeæ and semblis have filamentous or leaf-like processes at the sides of the abdomen. Among the diptera the larvæ of the chironomus have tracheæ and an aërial respiration; but the pupæ have branchial tufts on the thorax, and breathe by means of water. The anopheles, while in the larval state, has branchiæ at the caudal extremity; when a pupa it has tracheæ. Among the lepidoptera, the caterpillar of one moth, the botys stratiotalis, is aquatic. When the larvæ and pupæ, which breathe by means of branchiæ, undergo transformation, they lose

Respiratory organs of fishes.—In the osseous fishes there are four gills on each side, supported by the same number of branchial arches.* Each gill consists of a double series of lancet-shaped lamellæ attached to the branchial arch, like the teeth of a comb to its back. These lamellæ are frequently united for some distance at their base; they give off at right angles smaller lateral lamellæ. Each of the four branchial arteries, (see fig. 5) commencing its course at the inferior extremity of the branchial arch, runs in a groove along the convex border of the arch to its upper extremity, gradually diminishing in size; the veins run parallel with, but

the branchiæ and acquire stigmata, through which they inhale air. Representations of the branchiæ of aquatic insects, by Suckow, will be found in Heusinger's Zeitschrift für Organ. Physik, bd. ii.; and a more extended description of the respiratory organs of insects generally in Burmeister's excellent Entomologie.

* The structure of the gills of fishes has been thoroughly investigated by Rathke. (Untersuchungen über den Kiemenapparat und das Zungenbein der Wirbelthiere. Riga und Dorpat, 1832.) The following account is partly extracted from his work: [A great portion of the description of the respiratory apparatus of fishes and amphibia, having reference rather to comparative anatomy than physiology, has been omitted by the translator from the text and placed in the form of notes.]

1. *Skeleton of the branchial apparatus.*—The lower jaw of the osseous fishes is suspended to the os quadratum, which here consists of several pieces, with which three other bones belonging to the operculum are connected posteriorly.

Behind the lower jaw are the two hyoid arches, which consist each of several pieces, are connected by their external extremities to the os quadratum, and are united below in the middle line behind the root of the tongue; they have frequently a copula, or intermediate bone, between them, and under them the azygos portion of the hyoid bone. To the arches of the hyoid bone are attached the osseous branchiostegous rays, which support the opercular membrane. Behind the hyoid arches are situated, in the osseous fishes, four osseous arches,—the branchial arches,—to which the branchial lamellæ are attached like the teeth of a comb to its shaft. The highly vascular tissue of these lamellæ is supported by cartilaginous spines, which may be compared to the radii branchiostigi which arise from the hyoid arches, which have no branchiæ. The branchial arches consist of several, generally four portions; in the posterior arch there are not so many. In many osseous fishes there are, on the inner surface of the branchial arches, several small bony plates beset with small teeth. If the superior portion of the branchial arch on each side has many of these teeth, it is called the os pharyngeum superius. Between the arches of the one side and those of the other, where they meet each other, there are two or four bony or cartilaginous pieces, forming copulæ. Behind the last pair of branchial arches are the inferior pharyngeal bones, consisting of one piece on each side. They may be compared to a branchial arch without branchiæ. The branchial arches and pharyngeal bones are situated, in most fishes, under the cranium; in others, partly under the first vertebra. In the sharks and rays, the cartilaginous ossa quadrata support the lower jaw and the hyoid arches. Both the os quadratum and the hyoid arch have cartilaginous rays connected with them: those which are attached to the ossa quadrata correspond to the opercular bones; while those attached to the hyoid arch are analogous to the branchiostegous rays of the osseous fishes. The four cartilaginous branchial arches of the sharks and rays are situated under the commencement of the vertebral column, and consist of four segments. A cartilaginous plate, situated behind the branchial arches, corresponds to the

in the opposite direction to, the arteries, becoming larger as the latter become smaller, and, meeting on the vertebral column, unite to form the aorta. Each branchial artery gives off in the course just described as many branches as there are branchial lamellæ. These branches bifurcate twice, and terminate in the lateral capillary vessels of the smaller lamellæ, in which the veins take their rise and run in a corresponding manner on the opposite side of the branchial lamellæ.*

inferior pharyngeal bones of the osseous fishes. The branchial arches here, as in the osseous fishes, bear cartilaginous rays, directed outwards and backwards.

In the larvæ of the salamanders and frogs, and in the proteus family, the cartilaginous apparatus for the support of the branchia is, to a certain extent, formed of the same parts as in the fish. The os quadratum supports the inferior jaw, and generally the anterior cornu of the os hyoides also. The branchial arches do not consist of several segments, as in the fish; they are four in number, except in the proteus, in which there are but three; they are attached to the single or double posterior cornua of the os hyoides, which Rathke, however, regards as segments of the branchial arches.

During the transformation of the amphibia from the larva state, the cornua of the os hyoides of the frogs and salamanders do not disappear, but they undergo a change of form. Of the branchial arches there remains merely a rudiment of the first arch, which in the salamander becomes connected with the two cornua of the os hyoides. (Siebold, Observ. de Salamand. et Tritonibus.) In the cæciliæ the os hyoides has four pairs of arches throughout life. (See Rusconi, Della Circolazione delle Larve delle Salamandre.) It is remarkable that the cornua of the os hyoïdes in the lizards, even in the full-grown state, still present two, or even three pairs of arches. Rathke has made a corresponding series of observations on the embryos of mammalia, from which it results that in them the delicate branchial arches, as as already related at page 166, are at last reduced to the os hyoides; the hyoid arch becoming the anterior, the first branchial arch the second cornu of the os hyoides. It appears, however, that the branchial arches do not at all contribute to the development of the larynx, which is formed independently.

2. *Branchial opercula.*—In the osseous fishes the branchiæ are covered in by the opercular bones, which are connected with the os quadratum. In the sharks and rays, besides the cartilaginous radii which supply the place of the opercular bones, there are cartilaginous bands lying under the skin, parallel with the branchial arches, and forming an upper and an under series, so that the opercular bones of the osseous fishes are here, as it were, multiplied. These external opercular cartilages constitute, in the petromyzon, a very complicated external branchial skeleton; while the branchial arches themselves are wanting in these animals.

In the larvæ of the salamander, and in the proteus and axolotl, there is a lamina of the nature of a branchial operculum, but it contains no osseous or cartilaginous plates in its interior; the operculum of the larvæ of the frog is also merely membranous. This shows, as Rathke has pointed out, that the opercular bones attached to the os quadratum in fishes correspond to no bone in the higher vertebrata, and are, in fact, a structure peculiar to fishes. Least of all can they be compared to the auricular bones of higher animals. Huschke supposed that the auricular or ear bones were formed from portions of the branchial arches. But this is disproved by the fact which Windischmann observed, that in the axolotl there exist, simultaneously, branchial arches and two auditory bones, which are not contained in a tympanic cavity.

* Cuvier, Hist. Nat. des Poissons, tab. viii.

In the osseous fishes, and in the sturgeon, the branchiæ are unattached externally, being covered in merely by the moveable operculum, or, as in the eel, they are closed in by the branchial membrane, so as to leave a single opening only for the passage of the water.

In the sharks and rays there are four branchial arches, as in the osseous fishes; but from each arch a membrane extends to the skin, forming a septum between the different branchial cavities, of which there are five; these cavities are covered in externally by the skin, through which there is a separate opening into each. The branchial lamellæ arise from the arches, in the form of parallel folds of the mucous membrane lining the cavities. The first four cavities have each a single gill, or series of branchial folds, both on their anterior and posterior wall; the last cavity has but one branchia, namely, on its anterior wall. The gill on the anterior wall of the first branchial cavity is attached to the arch in front of the branchial arches; the succeeding single gills are situated on the surface of the membrane, separating the branchial cavities, and are connected, therefore, two with each branchial arch. The branchial cavities communicate internally with the pharynx.*

Branchiæ of amphibia.†—The respiratory organs of the tadpole are branchiæ. There is a branchial cavity on each side, and each cavity contains four branchial arches, from which branchial lamellæ arise. The branchial cavity on the right side is completely closed in by the skin; on the left side a small opening is left. The anterior extremities are developed in the branchial cavities.

* In the cyclostomata likewise there are branchial sacs with external openings, the sacs being formed by the union of two branchiæ. There are no branchial arches, and in their place there are merely membranous septa, which are invested with mucous membrane on both sides, at their posterior part. The branchial lamellæ are formed of thick folds of this mucous memærane. In the ammrrætes there are six, in the petromyzon there are seven of these branchial sacs and foramina. In the ammocœtes the internal branchial foramina open into the pharynx, in the same manner as the branchial clefts of the osseous fishes. In the petromyzon, however, the seven internal brancheal foraminæ opens into a branchus which lies in front of the œsophagus, and is closed posteriorly, but in front communicates with the mouth.

Ehrenberg has discovered in the sudis Ægyptiaca a spiral organ, connected with branchiæ, and of which the use is quite an enigma. In some fishes there are accessory branchiæ, as in the heterobranchus anguillaris, in which they are arborescent in form. In the anabus, and some other fishes which pass some time out of the water, they are wrinkled or plicated. In the fœtal state the sharks and rays have also filamentous external branchiæ, and it is remarkable that these organs project from the spout-hole in front of the os quadratum, which shows some analogy between this opening and the other true branchial foramina. On the branchial appendages, see Rathke, loc. cit.; the arborescent branchial appendages of the heterobranchus anguillaris are described in Burdach's Physiology, bd. iv. p. 161.

† On the structure of the respiratory organs of the larvæ of the caduci-branchiate amphibia, and of the proteidea, consult Cuvier, Oss. Fossil. t. v. 2. Humboldt and Bonpland, Beobacht. aus der Zool. Tübing. 1806. Rusconi, Configliachi del proteo

The larva of the salamander has external gills, with four branchial clefts. The proteus family have also external branchiæ, three in number, attached to branchial arches. In the siren (fig. 8), there are three branchial clefts on each side, in the proteus two, and in the axolotl four. The proteus family, throughout life, as well as the larva of the salamander and frog, in the second stage of their development, have both lungs and branchiæ, and consequently respire both air and water. The distribution of the branchial vessels of these animals is described at page 164.

The lungs of reptiles and amphibia are essentially mere sacs, of which the internal membrane is developed into folds, forming cells, so as greatly

Fig. 23.*

to increase the extent of surface (fig. 23). In most amphibia there is a membranous trachea leading to the lungs, but it is generally very short; in the anourous amphibia the larynx leads almost immediately into the membranous bronchi. The first appearance of cartilaginous plates in the bronchi is in the dactylethra, in which they form very irregularly branched and even perforated lamellæ, having no resemblance to bronchial rings. In the pipa, which is allied to the dactylethra, cartilaginous rings are met with. The bronchus of the cæciliæ has regular rings of cartilage.

In the true reptiles the respiratory surface is extended by increase of the number of cells in the interior of the lungs. (Fig. 23, *c*.)

In *birds* the lungs do not occupy the greater part of the thoracic cavity, as in mammalia. They lie at the posterior part, intimately connected with the ribs and bound down by the serous membrane, which lines the common cavity of the abdomen and thorax; for in birds the diaphragm is not developed. On the surface of the lungs there are openings, through which air passes from the bronchi into large cells, situated around the pericardium and between the viscera of the abdo-

anguino. Pavia, 1819. J. Müller's Beiträge zur Naturgeschichte und Anatomie der Amphibien. Tiedemann's Zeitschrift, iv. 2; and also page 163 of this work.

* [Diagram, showing the gradual development of the cellular lungs of reptiles. A. the upper portion of the lung of a serpent. The summit of the lung has cellular parietes; the lower part is a mere membranous sac. B. the lung of a frog, in which the cellular structure has extended over the whole internal surface of the lung, but is most considerable at the upper part. C. lung of the turtle,—the cells have extended so as to fill the interior of the lung.]

men. The bird can distend these cells with air, but cannot by that means render itself lighter for the purpose of flying.* The cells communicate again with the cavities of the bones, the majority of which are filled with air. The body of the bird is thus of course rendered specifically lighter than if its bones contained medulla. When a bird descends from a great elevation, where the air is rarefied, into a denser atmosphere, the air within its body very soon acquires the same tension as the surrounding air. Another peculiarity in the structure of the lungs in birds is, that their bronchi terminate in short blind cylindrical tubes, which lie side by side and have cellular parietes. In the embryo of the bird these tubes are still more distinct and more separated from each other, and have terminal dilatations. Retzius† remarks, likewise, that the bronchial tubes in birds communicate with each other.

In man and mammalia the structure of the lungs is essentially different. The minute bronchi have not the cellular parietes which we have described in birds, but terminate each in a distinct cell (fig. 24). These cells, or air vesicles, do not communicate one with another, their only opening is that of the minute bronchial twig which leads into each. Reisseisen§ has described a small artery, with its accompanying vein, going to each of these cells and forming around it a capillary net-work, which is so close that the diameter of the meshes is scarcely so great as that of the small vessels which form it. The diameter of a pulmonary vesicle is twenty times greater than that of one of the capillaries which are distributed in its parietes. The diameter of the pulmonary artery being $\frac{1}{6}$th smaller than that of the aorta,—their diameter being in the proportion of five to six,—the area of the pulmonary artery, in comparison with that of the aorta, must be in the proportion of twenty-five to thirty-six, or of about two to three. If, therefore, the smallest divisions of the pulmonary artery bear the same proportion to the trunk, as the capillary vessels of the body bear to the aorta, the united area of the capillary vessels of the lungs ought to occupy two-thirds of the space which the area of the capillaries of the rest of the body would comprise. It is very improbable, however, that this is the case; consequently the increase of capacity with which the ramification of the arteries of the body is attended must be much greater than that which takes place in the ramification of the pulmonary artery.

Fig. 24.‡

* This was shown by Kolhrausch, De Avium Saccorum Aëriorum Utilitate. Göttingen, 1832.

† Froriep's Not. 749.

‡ [Diagram to show the ramified form of the cavity of the lung of mammalia as contrasted with the sacculated cellular lungs of reptiles.]

§ De Fabricâ Pulmonum. Berol. 1822.

Respiration is effected by the contact of the air with the blood, the smallest particles of which, in its passage through the innumerable capillaries which ramify on the cells of the lungs, are, by means of the immense surface which all these cells offer, exposed to the action of the atmosphere. The chemical process which ensues between the air and the blood is carried on through the delicate membranous parietes of the cells, in accordance with the laws developed at pages 242—248.

CHAPTER III.

OF THE RESPIRATION OF MAN AND ANIMALS.

1. *Of respiration in the air.**

Changes produced in the air by respiration.—The earliest accurate experiments on respiration are those of Lavoisier and Seguin. They found that the air expired contained more carbonic acid and water, and less oxygen, than that which was inspired; the amount of carbonic acid gained being somewhat less than that of the oxygen which had disappeared. It being known that one volume of oxygen, united with carbon, forms one volume of carbonic acid, it was conceived that the greater part of the oxygen had united with the carbon of the blood, so as to form carbonic acid, which was expired in the gaseous form; while the rest of the oxygen, combining with hydrogen contained in the blood, had given rise to the watery vapour which is exhaled from the lungs in considerable quantity. Taking the mean result of the experiments of Lavoisier, Menzies, Abernethy, Thomson, and Hales, it would appear that the quantity of watery vapour exhaled by an adult in twenty-four hours amounts to 7,963 grains. This water contains some animal matter.†

Quantity of carbonic acid generated.—Sir Humphrey Davy having ascertained that a portion of air, which measured 161 cubic inches, was composed of 117 cubic inches of nitrogen, 42·4 cubic inches oxygen, and 1·6 cubic inch carbonic acid, respired it for the space of a minute, during which time he performed nineteen respirations. At the termination of the experiment he found the air to consist of 111·6 cubic inches nitrogen, 23·0 cubic inches oxygen, and 17·4 cubic inches carbonic acid. Consequently, 15·8 cubic inches of carbonic acid had been generated in his lungs in one minute.‡

Messrs. Allen and Pepys§ afterwards investigated the subject in an admirable manner; the air being inspired from one vessel and expired into another. As the mean result of their numerous observations they

* [Without omitting any of the facts which the author details in this chapter, the translator has placed them in an order which will, he thinks, make their connection, and the conclusions intended to be drawn from them, more evident.]

† Gmelin's Chemie, iv. p. 1524.

‡ Sir H. Davy, Researches on Nitrous Oxide, p. 435.

§ Philos. Transact. 1808, 1809. Schweigger's Journal, t. i. and Meckel's Archiv. iii. 233.

adopt their eleventh experiment, in which 302 cubic inches of carbonic acid were exhaled in eleven minutes, or about 27·2 cubic inches in one minute. After frequent repetition of their experiments, they found that air, after being once respired, contains 8 or $8\frac{1}{2}$ per cent. of carbonic acid; and that however often the same air is respired, even if until it will no longer sustain life, it does not become charged with more than 10 per cent. of this gas. This is illustrated by experiments 13 and 14. In the thirteenth experiment, which is particularly interesting, the fresh atmospheric air was contained in a vessel over water, the air expired was received into jars over mercury. After eleven jars were thus filled with expired air, the respiration of the air in the twelfth jar was continued, while the reservoir for fresh atmospheric air was being refilled. Twelve other jars were then filled as before, and this was repeated for a third time. The experiment occupied twenty-four and a half minutes. The air inspired during this period amounted to 9,890 cubic inches, that expired to 9,872 cubic inches. One hundred parts of the air expired were found, by analysis, to be composed of eight parts carbonic acid, thirteen parts oxygen, and seventy-nine parts nitrogen. Consequently, the whole amount of carbonic acid generated in the twenty-four and a half minutes would be 789·76 cubic inches, or 32 cubic inches in the minute. In the fourteenth experiment, 300 cubic inches of atmospheric air were respired for three minutes, but the carbonic acid generated amounted to 9·5 per cent. only. Thus, in the thirteenth experiment, in which fresh air was taken in at each inspiration, and in which 403 cubic inches of air passed through the lungs in a minute, 32 cubic inches of carbonic acid were formed in that time; while in the fourteenth experiment, in which the same air was respired repeatedly, and only 100 cubic inches passed through the lungs in a minute, the quantity of carbonic acid formed in the same space of time was only 9·5 cubic inches;—the quantity of air respired being, in the former case, 4 greater than in the latter, and the quantity of carbonic acid formed being also 3·3 times greater.

Allen and Pepys ascertained, moreover, that a man respiring oxygen generates more carbonic acid than when breathing common air. Thus, for 100 parts of oxygen inhaled, twelve parts of carbonic acid were expired; and a considerable quantity of nitrogen was developed at the same time.

Gmelin* has collected together the results of the different experiments of Davy, Berthollet, Allen and Pepys, Menzies, and Prout; and, taking the mean of all these, it would appear that 100 parts of air, once respired, contain 5·82 parts of carbonic acid.

Dr. Prout's† experiments seem to show that the quantity of carbonic acid generated in a given time is greatest between the hours of eleven, A. M. and one, P. M.; smallest between the hours of half-past eight, P. M. and half-past three, A. M. If the quantity of carbonic acid generated in

* Chemie, iv. 1525. † Ann. Phil. vol. ii. p. 330, and vol. iv. p. 331–334.

respiration is from any cause increased for a period, it afterwards sinks in the same proportion below the usual quantity. The amount of carbonic acid exhaled by the same person, is diminished by depressing passions, violent exercise, by taking spirituous liquors, tea, or vegetable food, and by the long-continued use of mercury. The carbonic acid is exhaled in larger quantity when the barometer is low.

The quantity of carbonic acid formed by the process of respiration in twenty-four hours is estimated by Lavoisier and Seguin to be 14,930 cubic inches, or 8,534 grains; Davy estimates it at 31,680 cubic inches, or 17,811 grains; and Allen and Pepys at 39,600 cubic inches, or 18,612 grains. The quantity of carbon thus removed from the blood would be, consequently, according to Lavoisier's calculation, 2,820 grains; according to Davy's estimate, 4,853 grains; and 5,148 grains, according to the calculation of Allen and Pepys. In all these calculations, the quantity of carbonic acid is, as Berzelius remarks, evidently too great; for the solid food taken into the body contains three-fourths of its weight of water, and of the other fourth seldom more than half is carbon; consequently, six and a quarter pounds of solid food would be necessary to supply the quantity of carbon which, according to these estimates, is excreted from the body by the lungs in twenty-four hours, independent of what is got rid of in other ways.

Amount of oxygen consumed.—Davy, Pfaff, Berthollet, and Allen and Pepys, all agree that the air, once respired, is diminished in volume. Allen and Pepys attributed this loss, which they estimated at not more than $\frac{1}{122}$ of the whole, to accidental circumstances. When the same air is respired repeatedly, as long as it can be borne, the diminution in volume is very distinct; taking the mean of the estimates which have been given by Lavoisier, Goodwin, Davy, Allen and Pepys, and Pfaff, it would be $\frac{1}{24}$th of the volume of the air inspired.*

Allen and Pepys state that when the same atmospheric air was respired several times, the amount of carbonic acid generated was less than that of the oxygen which disappeared; for instance, in one hundred parts of the expired air, eighty-six parts were nitrogen, four oxygen, and ten carbonic acid: they suppose that a part of the carbonic acid is retained by the blood. But the same experimenters state that in the respiration of atmospheric air by guinea pigs,† the quantity of oxygen lost was exactly replaced by the carbonic acid generated; although, when pure oxygen was used in the experiment, more oxygen was absorbed than was accounted for by the carbonic acid produced, the deficiency in this case being supplied by nitrogen; and when the gas respired consisted of oxygen and hydrogen, in the proportions in which oxygen and nitrogen exist in the atmosphere, the result was the same as when pure oxygen was employed.

In experiments instituted twenty years afterwards, on pigeons, Allen

* Gmelin's Chemie, iv. p. 1525.

† Meckel's Archiv. iii. tab. v.

and Pepys obtained the same result from the respiration of pure oxygen; more oxygen was absorbed than the quantity of carbonic acid expired accounted for.

Dulong* placed the animals in an apparatus from which the air could be constantly removed, and new air supplied, so that the experimenter could ascertain the changes that were produced in the proportion of the different gases composing the air. He found that during the respiration of all animals,—carnivorous and herbivorous, mammalia and birds,—more oxygen is consumed than is replaced by the carbonic acid formed. The quantity of oxygen thus lost, and not replaced by carbonic acid, amounted, on an average, in the case of herbivorous animals, to $\frac{1}{10}$th of the volume of that which was replaced by carbonic acid; in the case of carnivorous animals it amounted to from $\frac{1}{5}$ to $\frac{1}{2}$.

The results of the experiments of Despretz† are the same, namely, that a part of the oxygen is lost; the carbonic acid formed amounting to $\frac{2}{3}$rds or $\frac{3}{4}$ths only of the oxygen which had disappeared.

The results of most experiments which have been made on the subject seem to leave no doubt but that less carbonic acid is formed during respiration than will replace the oxygen which disappears. Allen and Pepys, who are the only observers that failed to perceive this difference during ordinary respiration, did not consider that atmospheric air already contains a small proportion of carbonic acid, which alone would make a considerable difference in the results.

Is the proportion of nitrogen in the air changed by respiration?—During the respiration of man and the higher animals, the nitrogen of the atmosphere seems to be, under some circumstances, absorbed, and in other circumstances exhaled.

1. Sir H. Davy‡ states that in his experiments, an absorption of nitrogen took place to the amount of $\frac{1}{17}$th of the volume of the oxygen which disappeared from the atmosphere, so that, in twenty-four hours, it was as much as 2,246 grains. Pfaff§ also observed a diminution in the quantity of the nitrogen; and estimated it at from $\frac{1}{107}$th to $\frac{1}{80}$th of the volume of the air inspired.

2. Other experimenters,—Allen and Pepys, for example,—perceived neither increase nor diminution in the proportion of the nitrogen when atmospheric air was respired.

3. Several observers, as Berthollet, Nysten, Dulong, and Despretz, have, on the other hand, detected an increase in the proportion of nitrogen in atmospheric air during respiration. It was most marked in the experiments instituted by Despretz, who found it to be general, but

* Schweigger's Journal, xxxviii. 505.

† See the account of Despretz's experiments at page 84.

‡ Researches on Nitrous Oxide, pp. 431–438. Gilbert's Annal. xix. 298.

§ Gehler's Journal der Chemie, v. 103.

more considerable in herbivora than in carnivora;—this last circumstance seems extraordinary, for the food of herbivorous animals contains less nitrogen than that of carnivorous animals. The volume of nitrogen thus added to the atmosphere is stated by Despretz to be equivalent to from $\frac{1}{7}$th to $\frac{11}{7}$ths of that of the oxygen which disappeared from the air and was not replaced by carbonic acid. The fact of nitrogen being developed in the lungs may be best determined by making animals respire an air which contains no nitrogen; and this has, in fact, been done by Allen and Pepys, who ascertained that when guinea-pigs are made to breathe in a mixture of hydrogen and oxygen, nitrogen is exhaled, and in a quantity exceeding the volume of the whole body of the animal, which shows that it could not be derived from the air previously contained in the lungs.

4. The conclusion to be deduced from all these experiments seems to be that during respiration nitrogen is both absorbed and exhaled by the blood; and that it is from the exhalation of the nitrogen being counterbalanced by its absorption, that this exhalation is not observed, except when the air respired, itself, contains no nitrogen. The discrepancy in the results obtained by different experimenters in regard to this point, is explained by M. Edwards,* by supposing that under certain circumstances the absorption of nitrogen is most active, under other circumstances the exhalation.

M. Collard de Martigny,† who found an increased proportion of nitrogen in air which had been respired, also observed an exhalation of nitrogen by the skin. On the ground that nitrogen, like all other gases, is imbibed by moist animal membranes and by the skin, M. Collard assumes that absorption and exhalation of nitrogen go on at the same time in the lungs, but that the exhalation is most active. Berzelius‡ regards the idea of a simultaneous exhalation and absorption of nitrogen as absurd.

Respiration of cold-blooded animals.—I have instituted several experiments on frogs, to ascertain the quantity of carbonic acid formed by the respiratory process in these animals.

Their lungs being emptied and the throat compressed, the frogs were introduced into a graduated cylinder, over mercury, and the quantity of carbonic acid generated was ascertained by the diminution which took place in the volume of the gas when potash was introduced. In the first experiment, a frog, weighing 440 grains, placed in a cylinder which contained ten cubic inches of atmospheric air, generated $\frac{2}{3}$rds of a cubic inch of carbonic acid in six hours. In the second experiment, a frog, which weighed 655 grains, formed $1\frac{1}{4}$ cubic inches of carbonic acid in eight cubic inches of atmospheric air in the period of twelve hours,

* Ann. de Chim. et de Phys. 22, 35. Influence of Physical Agents, &c. p. 226–229.
† Journ. de Physiol. 1830.
‡ Jahrb. iv. 217.

the barometer standing at 30 inches 1 line, the thermometer at $54\frac{1}{2}$° Fahr. In the third experiment, a very large frog, weighing 1,260 grains, was confined in $16\frac{5}{6}$ cubic inches of atmospheric air, at a temperature of $45\frac{1}{2}$° Fahr., the barometer being at 29 inches 3 lines; it generated two cubic inches of carbonic acid.

Having reduced the results of these experiments to the same circumstances, namely, a period of six hours, a temperature of $65\frac{3}{4}$ Fahr., and an atmospheric pressure of 30 inches 4 lines, I found that the quantity of carbonic acid formed in the above period by a frog weighing 440 grains, was 0·66 cubic inches; by a frog weighing 655 grains, 0·63 cubic inches; and by one which weighed 1,260 grains, 0·88 cubic inches. These three results, together with those of three experiments by M. Edwards,* afford, as is shown by the following table, 0·57 cubic inch, or rather more than half a cubic inch, as the quantity of carbonic acid formed by the respiration of a single full-grown frog in six hours.

	Observer.	*Quantity of Carbonic Acid formed in 24 hours, at $65\frac{3}{4}$ F. by a single frog.* Cubic Inches.	*Quantity of Carbonic acid formed in six hours.* Cubic Inch.
1st Experiment	M. Edwards	2·55	0·63
2nd do.	Do.	1·30	0·32
3rd do.	Do.	1·25	0·31
1st do.	Prof. Müller		0·66
2nd do.	Do.		0·63
3rd do.	Do.		0·88
	Mean of the Six Experiments		0·57

From the results of my three experiments, I have again calculated the quantity of carbonic acid formed in 100 minutes for every 100 grains of the animal; and comparing the numbers thus obtained, with some experiments on frogs and toads by Treviranus,† who had reduced his results to the same circumstances of temperature and atmospheric pressure, and also calculated them for 100 grains of the animal, and for 100 minutes of time, (as is done in the table which follows,) it would appear that for every 100 grains of a frog or toad, $\frac{1}{20}$th of a French cubic inch of carbonic acid is formed in 100 minutes.

Species of Animal.	*Observer.*	*Quantity of Carbonic Acid exhaled in 100 minutes for every 100 grains of the animal.*
Bufo cinereus, A.	Treviranus	0·02
Bufo cinereus, B.	Treviranus	0·03
Rana temporaria, A.	Treviranus	0·10
Rana temporaria, B.	Treviranus	0·14
Frog, A.	Müller	0·041
Do. B.	Müller	0·027
Do. C.	Müller	0·019
	Mean	0·054 Cubic inch.

* Influence des Agens Phys. &c. p. 648. † Zeitschrift für Physiologie, iv. H. i. p. 23.

Treviranus has also investigated in an excellent manner the respiration of the lower animals, and reduced the results to the same standard, with regard to heat, atmospheric pressure, time, and weight of the animal, as in his experiments on frogs and toads; and from his calculation it appears that, in proportion to their weight, avertebrate animals generate as much carbonic acid as the amphibia.

Comparison of the products of the respiration of cold-blooded and warm-blooded animals.—From the results obtained by different observers, in experiments on the respiration of birds and mammalia, Treviranus has calculated the numbers corresponding in the several cases to 100 minutes of time, and 100 grains weight of the animal.

Animal.	*Observer.*	*Carbonic Acid.* Cubic Inch.	*Oxygen absorbed.* Cubic Inches.
Guinea-pig	Berthollet	0·42	0·67
Do.	Allen and Pepys	0·60	0·74
Do.	Despretz	0·47	0·68
Rabbit	Berthollet	0·44	0·60
Cat	Despretz	0·66	0·98
Pigeon	Despretz	0·99	1·58
Do.	Allen and Pepys	0·96	1·14

Taking the mean of the data afforded by this table, it appears that for every 100 grains weight of a mammiferous animal 0·52 French cubic inch [0·62 Engl. cub. in.] carbonic acid is formed in 100 minutes, and for every 100 grains of birds 0·97 French cubic inch [1·16 Engl. cub. in.] in the same space of time. We have already seen that, according to the results of the experiments of Treviranus and myself, 0·05 French cubic inch [0·06 Engl. cub. in.] of carbonic acid are exhaled by frogs and toads in 100 minutes for every 100 grains of their weight; consequently the quantity of carbonic acid generated by cold-blooded animals is ten times less for the same weight of the animal than is formed by the respiration of mammalia, and nineteen times less than is generated by birds.

Treviranus has found, that in most insects the carbonic acid generated by respiration is, in proportion to their weight, in as great quantity as in mammalia, although in some cases it approaches the proportion observed in amphibia. The small amount of animal heat developed by insects cannot, then, be explained by the proportion of the carbonic acid formed in the respiratory process; but Treviranus supposes that their low temperature may arise from heat becoming latent in them during the developement of the nitrogen which they exhale in large quantity.*

But even if the results of experiments on insects be rejected on account of their being subject to error from the small size of the animal, still, even in the case of mammalia and amphibia, the difference of temperature cannot, with any probability of truth, be referred to the differ-

* [See the note on the temperature of insects at page 94, and Mr. Newport's paper on the respiration of insects in the Philos. Transact. for 1832.]

ence in the quantity of carbonic acid generated in the two orders of animals.*

The experiments of Treviranus seem to show that the generation of carbonic acid by the lower animals is influenced by the temperature of the medium in which they respire. At $81\frac{1}{2}°$ Fahr. a honey-bee exhaled nearly three times as much carbonic acid as it did at $58\frac{1}{2}°$. In general, the carbonic acid generated during respiration in the open air was insufficient to replace the oxygen absorbed. The quantity of oxygen consumed in the respiration of cold-blooded animals was often three times as great as that of the carbon exhaled.

Molluscous animals, however, do not merely extract all the oxygen from the air in which they are placed; they continue after this to exhale carbonic acid. Treviranus observed in all his experiments on the lower animals that nitrogen was exhaled, and in a few cases its quantity even exceeded that of the carbonic acid formed.

2. *Of respiration in the water.*

Changes produced in the water by the respiration of fishes.—The question of the exhalation or absorption of nitrogen during respiration† is rendered still more complicated by the fact observed by Humboldt and Provençal, namely, that fishes absorb a considerable quantity of azote from the water in which they respire. Some fishes were kept during eight hours and thirty minutes in 4000 cubic centimeters of water. Before the experiment 2582 parts of the water contained 524 parts of air; after the experiment the same quantity of the water yielded only 453 parts of air. Humboldt and Provençal attribute this loss of 71 parts of air to the effect of respiration; and from the difference of the constitution of the air before and after the experiment, they calculate the proportion of the gases which had been absorbed or exhaled. In the 524 parts of air contained in the water which had not been subject to respiration, 155·9 parts were oxygen, 347·1 nitrogen, and 21·0 carbonic acid; in the 453 parts of air obtained from the water which had been respired, 10·5 parts were oxygen, 289·3 nitrogen, and 153 carbonic acid. Consequently, 145·4 parts of oxygen and 57·6 parts of nitrogen had been absorbed, while 132 parts of carbonic acid had been exhaled. Treviranus imagines that the portion of air, namely 71 parts, which was here removed from the water by the fishes, had been taken with the water into the stomach. Humboldt and Provençal‡ did not, however, observe any loss of hydrogen, when the water in which the fishes respired was impregnated with a mixture of oxygen and hydrogen in place of atmospheric air.§

The experiments of the same physiologists show, moreover, that fishes absorb more oxygen than is replaced by the carbonic acid exhaled,

* See page 85.

† See page 309.

‡ Mém. d'Arcueil, t. ii.

§ Schweigger's J. i. p. 111.

which amounts, at most, to $\frac{4}{5}$ths, and frequently to $\frac{1}{2}$ only, of the oxygen absorbed.

It appears, from their researches, that fishes in rivers are, with reference to the quantity of oxygen in the medium which they respire, in the same condition as an animal breathing in an atmosphere that contains less than one per cent. of oxygen; for water never contains more than $\frac{27}{1000}$ of its volume of air, of which 31 per cent. is pure oxygen.

Treviranus has calculated from the results of the experiments of Humboldt and Provençal that a tench generates, in 100 minutes, for every 100 grains of its weight, $\frac{12}{1000}$ths of a cubic inch [English] of carbonic acid; and, consequently, since in the same space of time $\frac{62}{100}$ths of a cubic inch [English] of that gas are exhaled by a mammiferous animal for every 100 grains of its weight, mammalia appear to generate fifty times more carbonic acid than fishes.

Respiration of fishes by the skin.—Fishes absorb oxygen and exhale carbonic acid, not merely with their gills, but with the whole surface of their body, as long as they are surrounded with water impregnated with atmospheric air,—not when they are exposed to the air itself. To prove that fishes respire by the whole surface, Humboldt performed the following experiment. He passed a cork collar, covered with waxed cloth, over the head of a fish, which was then introduced into a cylindrical vessel filled with Seine water, the vessel being closed by the cork collar, which was so adjusted that the head and gills of the fish did not come into contact with the water in the vessel. Fishes thus treated lived five hours, and the water in the vessel underwent the changes usually produced by respiration.

Respiration of fishes in the air.—As long as the gills are kept moist, fishes will continue to respire in the air, and will absorb the same quantity of oxygen, neither more nor less than by respiration in the water. Thus a tench reduced 133·9 cubic centimeters of atmospheric air, in nineteen hours and a half, to 122·9 centimeters, and had absorbed from it 0·52 cubic centimeters of oxygen. Aquatic respiration differs then from respiration in the air less essentially than might at first appear. A moist surface is necessary even in pulmonary respiration.

Ermann states that the cobitis fossilis, which lives chiefly in the mud, comes to the surface to swallow air, which subsequently undergoes in the intestines the usual changes produced by respiration, and is afterwards evacuated by the anus.*

* The *swimming bladder* of fishes also contains air, of which one component is oxygen; but this air is not derived from without; it is secreted by the inner surface of the sac. The proportion which the oxygen bears to the nitrogen is sometimes greater, sometimes less, in the air of the swimming bladder than it is in the atmosphere. In the air of the swimming bladder of fishes of inland lakes, Ermann (Gilbert's Annal. xxx. 113,) found but a small proportion of oxygen. From the air of the air-bladder of

Many animals which respire by means of branchiæ in the water, produce remarkable currents in the water around the branchiæ. These currents are now known to be produced by the vibration of minute cilia, and the phenomenon is called ciliary motion.*

3. *Of the respiration of the embryo of animals.*

The embryos even of frogs and toads, of sharks and rays, and of the sword-fish, are provided with external branchiæ; and the whirling motion of the embryos of mollusca in the ovum seems to prove that they have respiratory organs by the action of which currents are produced in the water.

The ova of oviparous animals during their developement effect the same changes in the surrounding air as the adult animals; and they are not developed, if the supply of atmospheric air, or of water impregnated with it is prevented.

Respiration of the embryos of birds and insects.—The embryo in the egg of the bird perishes, if the shell is covered with varnish or oil.

fishes which live in the depths of the ocean, Biot (Gilbert's Annal. xxvi. 454,) obtained from 69 to 87 per cent. oxygen; while the air with which the water of the ocean at a considerable depth was impregnated, contained only 29 parts oxygen, and 71 parts nitrogen in 100 parts. The composition of the air varies, however, even in the same species of fish. In spring and summer the air is said to contain less oxygen than in autumn; and sometimes it contains no oxygen. (See Delaroche, Schweigger's Journ. i. 164, and Configliachi, ibid. 137.) According to the mean result of a great number of experiments instituted by Humboldt and Provençal, the air of the swimming bladder of the carp would consist of 71 parts oxygen, 52 parts carbonic acid, and 877 parts nitrogen in 1000 parts. In many fishes, as in the carp, the air-bladder communicates with the pharynx. The tube which leads from the air-bladder sometimes opens into the pharynx by a wide orifice; sometimes, as in the carp, the opening is so narrow that no air can enter the tube from the pharynx, and it is, probably, only when the bladder is much distended that any air can force its way out of it. In many fishes the communication does not exist at all, and in them there is usually a red vascular and peculiar tissue in the walls of the bladder, destined for the secretion of the air; and even when the air-bladder does communicate with the pharynx, it is most probable that the air is secreted. In the sciænæ the air-bladder has several cœca, which in some species are ramified. (Cuvier, Hist. Nat. des Poissons, tab. 138, 139.) E. H. Weber has discovered in several fishes of the genera cyprinus, cobitis, sparus, and clupea, a connection between the air-bladder and the organ of hearing; this will be spoken of in another part of the work. Rupture of the air-bladder does not always deprive the fish of the power of maintaining its balance,—the fish does not always fall upon the side. The air-bladder is probably intended to enable the fish to alter its specific gravity, which it may by compressing the air by means of the abdominal parietes, and on the other hand increasing the distension of the bladder. (See G. Fischer, über die Schwimmblase der Fische. Leipz. 1795. G. R. Treviranus, Vermischte Schriften, 2 bd. 156.)

* [A full account of the recent discoveries relative to the ciliary motions is given in the fourth book. The subject was imperfectly known when this part of Professor Müller's work was published; the translator has therefore omitted what was here said respecting it.]

In warm water also the developement of the egg of birds is not maintained, nor in irrespirable gases according to Viborg's* experiments; Ermann† has stated, on the contrary, that when the eggs were kept at the proper temperature in irrespirable gases, the embryos were developed. Schwann‡ has, however, made some very accurate experiments which confirm Viborg's results. He has shown that when eggs of the common hen are kept at the proper temperature in gases which contain no oxygen, the enlargement of the germinal membrane, its division into serous and mucous membrane, and the formation of the area pellucida, take place, but that neither blood nor embryo are formed. Eggs which had been kept in hydrogen at the heat of incubation for twenty-four hours, if supplied with atmospheric air, at the end of that time were developed; but the result was different if the period of their confinement in hydrogen was extended to thirty hours or more. It appears from Michelotti's experiments on the eggs of insects, that during their developement the air is chemically changed as long as its temperature is between 65° Fahr. and 77° Fahr.; but that under 32° Fahr. these changes in the air are not effected. In irrespirable gases the embryo insect is not developed.§

The atmospheric air has such free access to the ovum through the pores of the shell of the bird's egg, that it is almost impossible that the air should not be acted on by the blood in the vessels of the allantois; the chief function of the allantois would indeed seem to be to bring a large number of blood-vessels as near the surface as possible. The water of the white of the egg is constantly evaporating, and with a rapidity which seems to be nearly the same whether the egg be subject to incubation or not. The evaporation of the water diminishes the volume of the albuminous fluid,—or white,—which becomes separated further and further from the shell at the large end of the egg, the space being filled by air which enters through the pores of the shell. Bischoff‖ analyzed the air which fills this space in the egg, and found it to contain more oxygen than atmospheric air, the proportion of oxygen varying in different eggs from 22 to $24\frac{1}{4}$ per cent. Dulk also found the proportion of oxygen to be from $25\frac{1}{4}$ to $26\frac{3}{4}$ per cent.; but, after incubation, it was reduced to 17·9 per cent., and 6 per cent. carbonic acid was added to the air.¶

Respiration of the embryo of mammalia.—The first stages of the developement of the ovum of mammalia take place not merely without the

* Abhandl. für Thierärzte und Œconomen. iv. 445. † Isis, 1818.

‡ De necessitate aëris atmosph. ad evol. pulli in ovo. Berol. 1834. Mueller's Archiv. 1835, p. 121.

§ Pfaff und Friedlander, Französ. Ann. 4. H. 48. Burmeister, Entomol. 365.

‖ Schweigger's Journ. N. R. ix. 446.

¶ Schweigger's J. 1830. i. 365. Berzelius, Jahresb. xi. 336.

access of atmospheric air, but even before the ovum has any connection with the parent, and when it is merely surrounded by the secretions of the uterus. The ova of mammalia do not respire in the ordinary sense of the term; but the function of respiration is in them supplied by their connection with the parent animal. E. H. Weber has demonstrated by some very interesting dissections the manner in which the placenta and uterus are connected in the human subject, and has shown that in man, as well as in ruminating animals, no direct communication exists between the vessels of the fœtus and those of the mother.*

There are several circumstances which render it probable that the placenta performs a function analogous to the respiration of the ova of oviparous animals.

Thus, in the first place, interruption of the circulation in the umbilical vessels causes the death of the ovum; secondly, respiration is necessary to the ova of oviparous animals, and is effected by the allantois membrane, which receives the same vessels, as the chorion of the ovum of man and mammalia, namely, the umbilical vessels; and the third circumstance is, that in the same order of animals, both oviparous and viviparous genera occur. Thus the ova of the majority of serpents and lizards are developed in the air; the ova of the lacerta crocea, of the blind worm, and vipers, in the oviduct. Even in the ova of the lizard the developement of the embryo is far advanced before the eggs are deposited. It appears, therefore, that in the oviduct in which the ova of the vipers are developed without any immediate connection with the parent animal, the want of the respiration enjoyed by the ova of other reptiles is supplied by the secretion of a peculiar fluid, as seems to be the case likewise in mammalia. This is confirmed by the fact that the external covering of the ova of these viviparous reptiles, the lacerta crocea, and vipers, is a delicate membrane, while in oviparous lizards and serpents it is a solid shell.†

Change produced in the blood of the fœtus during its passage through the placenta.—The function, however, which in mammalia replaces the respiration of the ova of other animals, must be a very peculiar process; for there is no perceptible distinction of colour between the blood of the umbilical arteries and that of the umbilical veins. If the umbilical veins were perfectly analogous to the pulmonary vein, and the umbilical arteries to the pulmonary arteries, which in frogs and salamanders are really branches of the aorta, the blood of the umbilical vein should be of a brighter colour than that of the umbilical arteries, and than that of the arteries and veins of the body of the fœtus generally. Haller, Hunter, and Osiander never observed such a difference of colour in the blood of these vessels; nor have Autenrieth and Schuetz ‡ perceived it in

* See page 249. † V. Baer, Meckel's Archiv. 1828. 573.

‡ Exp. circa calorem fœtus et sanguinem. Tüb. 1795.

rabbits, nor Emmert* in guinea-pigs. Blumenbach and Emmert have, however, perceived some difference of colour in the vessels of the chorion of birds; and Herrissant and Diest,† and Bandelocque,‡ declare that they have perceived a difference of colour in the two kinds of blood of the fœtus. Bichât in one place§ denies it, and in another place says,‖ that the difference is not great in guinea-pigs. I have myself, also, some years since failed in detecting any difference of colour between the blood of the umbilical arteries and that of the vein in the fœtus of the cat, rabbit, and guinea-pig. Small animals are indeed as well or even better adapted for the observation than larger animals. At the same period, however, when as a student I was paying attention to this subject, I once fancied that I could perceive this difference between the two kinds of blood in a sheep which was opened during life; and others who were present also believed that they saw it. Joerg¶ likewise states that he has perceived a difference of colour in the vessels of the chorion of the horse. But my later observations agree with those which I made on the smaller animals. Many female sheep are slaughtered at Bonn; so that during the first part of the winter the embryo of sheep and even of cows can be obtained easily, together with the uterus, and often while they are warm. During the winter such parts were brought to me regularly for anatomical purposes, and I have not a second time observed a distinct difference in the colour of the blood of the umbilical vein and arteries. E. H. Weber** also denies that this difference exists, and those who practise midwifery have not observed it.

The distinction of colour of the venous blood of the body, and that returning from the lungs, is in reptiles so marked, that they can be distinguished by their colour in the right and left auricle, and even when partly mixed in the ventricle. In fishes, however, I have hitherto certainly not remarked any difference in the two kinds of blood; perhaps this is accounted for by the circumstance that the medium which they respire contains only 1 per cent. of oxygen, while the atmosphere contains 21 per cent.

The blood of the umbilical vessels of the fœtus, like the venous blood of the adult, is reddened by exposure to the air. This I have frequently observed: it may perhaps take place a little slower and in a less marked degree than venous blood, as Fourcroy observes. The blood of the umbilical vessels and that of the fœtus also coagulates less firmly than that of the adult. This circumstance was remarked by Fourcroy, and I have myself frequently observed it. In opening a living sheep in a pregnant

* Reil's Archiv. x. 122.

† Haller's Disp. v. pp. 516. 526.

‡ Bichât's Anat. Générale, ii. 465.

§ Loc. cit. p. 343.

‖ Loc. cit. p. 465.

¶ Die Zeugung. Leipz. 1815. 273.

** Hildebrandt's Anat. Bd. iv. 524.

state, I noticed that the blood of the umbilical vein, which was collected in considerable quantity, coagulated more slowly than that of the umbilical arteries; but this might probably arise from the blood of the vein being collected first, while the blood of the arteries had advanced towards coagulation before it was drawn from the vessels. I also observed in my earlier experiments that the blood from the umbilical vessels of a fœtal cat, when allowed to flow into a glass filled with carbonic acid gas, became of a dark violet colour. I have recently confirmed this observation by repeating the experiment with the blood of a fœtal sheep. It is another point of resemblance between the fœtal blood and the venous blood of the adult, the colour of which is likewise rendered darker by exposure to carbonic acid. Exposure to the vacuum of an air-pump produces no change in the colour of the blood of the umbilical vessels; and my more recent experiments convince me that I was in error when, in my earlier observations, I thought I saw it become slightly darkened in colour while in the vacuum of the air-pump.

If the blood of an adult is gradually heated to 200° Fahr., consequently above the heat at which albumen coagulates, in a vessel provided with a tube to carry off any gas that might be developed, no oxygen or carbonic acid is obtained, and the air which passes over by the tube is that which was previously contained in the vessel and the tube. Sir H. Davy must have been deceived in his early experiments, from which he concluded that a developement of gas takes place under these circumstances; and many physiologists have fallen into the same error. I performed the experiment with blood taken from the umbilical vein of a pregnant sheep while the animal was still alive, and the result was of course the same. Air passed over by the tube, but it was merely the unchanged air previously contained in the vessel. Again, I heated the watery solution of blood obtained by cutting into pieces, under warm water, the umbilical vessels and placenta of a fœtal cat, but no gas was developed.

Sir H. Davy states that he once observed a developement of oxygen from fresh arterial blood of a calf which was exposed to the light of the sun at a temperature of from 108° to 200° Fahr. in a glass tube of which one end was closed and the other inverted in blood of the same kind.* Some time since I opened a pregnant cat while alive, received the blood of the divided umbilical vessels in water, and cut the placenta into pieces in the same water. With the bloody fluid thus obtained, I filled a short glass tube closed at one extremity, inverted the open end in some of the same fluid, and exposed it to the light; but no developement of gas was perceptible. I have more recently repeated the experiment with the blood of the umbilical vein of the fœtal sheep, heating the

* Beddoes's Contributions, p. 182.

apparatus in the same gentle manner, but perceived no developement of gas in the tube. Even with the arterial blood of an adult, the experiment is not attended with the result obtained by Davy. There must have been some source of error in his mode of performing the experiment; perhaps some gas had become mechanically mixed with the blood.

It appears, then, that the blood of the fœtus, both arterial and venous, differs in no perceptible respect from the venous blood of the adult.

Does the liquor amnios serve the function of respiration?—Some physiologists have maintained that the liquor amnios with which the fœtus is surrounded serves the purpose of respiration by the skin of the embryo; or even, because some of the fluid has been found in the trachea, they have supposed it to be respired by the lungs.* Leclarc and Geoffroy St. Hilaire have adopted this opinion; and the discovery of Rathke that processes resembling branchial arches exist in the neck of the fœtus of vertebrate animals, has led others to imagine that these processes also might serve the respiratory function. The delicate processes separated by the branchial clefts can be distinctly seen, according to my observation, only during the first days of the embryonic life of the chick,—for instance, on the third or fourth day,—and they are merely the framework common to all vertebrata, on which in fishes, and those amphibia which have branchiæ during their larval state or throughout life, the true branchial lamellæ are developed; the developement never takes place in other animals, and the arches are converted into the cornua of the os hyoides.† The experiments which I made when a student, showing that fishes do not live longer in the liquor amnios of the cow and sheep than in oil,—namely, four minutes,—while in the same quantity of Rhine water they live a long time, would alone indicate that this fluid, the liquor amnios, cannot serve the purpose of respiration. Lassaigne's experiment, which seemed to show that the liquor amnios of a sow contains air, which in its constitution of oxygen and nitrogen very much resembles atmospheric air, must have been inaccurately performed, or the liquor amnios must have absorbed air from the atmosphere, either from the ovum having been long exposed to it, or from the fluid itself having remained in a vessel a long time exposed to the air. Not being satisfied with my early inaccurate experiments, which indeed led me to the conclusion that the liquor amnios contains no air, I eagerly embraced the opportunity of investigating this point in an accurate manner. For this purpose, to avoid the error which, in the use of a vessel with a tube to conduct away the gas formed, might arise in calculating the quantity of air previously contained in the vessel, I filled with the liquor amnios of the sheep a jar ten inches long and one and a half inches broad, which would contain seventeen cubic inches, and which was graduated in cubic inches, and inverted it in a vessel containing the same

* Scheel, De liq. amnii nat. et usu. Hafn. 1799.

† See note page 302.

fluid. I then filled the exterior vessel with warm water, and heated the whole apparatus to the boiling point. If any gas or air had existed in the liquor amnios, it must have collected at the upper extremity of the tube; but with the exception of the vapour of water, which very quickly condensed again and disappeared, the only gas developed was a very small quantity in the form of foam, which did not amount to $\frac{1}{8}$th of a cubic inch. In a second and third experiment the result was the same, and no more air was developed when I continued the boiling for a longer period. Professor Bergemann was present, and was convinced that no air is developed under these circumstances. In a fourth experiment I did indeed obtain a small quantity of gas, which did not disappear when the fluid cooled; but its volume was very small, and did not amount to $\frac{1}{8}$th of a cubic inch, the quantity of the fluid being 17 cubic inches. Agitating it with lime-water or solution of sulphuret of potash did not diminish its volume, consequently it did not contain any oxygen or carbonic acid.*

I may add, that in my earlier experiments I found that the fœtus of rabbits, about four inches long, taken from the uterus of the living animal, and placed under the exhausted bell of the air-pump, whether their membranes had been opened or not, ceased at the expiration of fifteen minutes to present signs of life, but recovered their power of motion when again exposed to the air. This, however, proves nothing in reference to respiration. It only shows the effect of removing atmospheric pressure.

CHAPTER IV.

OF THE CHANGES WHICH THE BLOOD UNDERGOES IN THE LUNGS.†

Its colour.—By respiration the blood is rendered of a bright red colour. The same change of colour is produced by agitating the blood with oxygen, and on the surface of venous blood by mere exposure to the air. This bright scarlet colour may also be given to blood by the admixture of sugar, or of neutral salts,—such as nitrate of potash, sulphate of soda, sal-ammoniac, muriate of soda, and carbonate of potash. Solution of potash, according to my observation, changes the colour of the blood to brown, although the contrary is erroneously stated in some works. Thenard and Huenefeld state, that the blood acquires a cherry-red colour when exposed to an atmosphere of ammonia. Chlorine changes its colour first to brown, then to white; by acids generally it is rendered brown; but carbonic acid first darkens its red colour, then changes it to violet, and at last renders it almost black. Wedemeyer says, that prussic acid brightens the red colour of the blood; but Hertwich‡ asserts that it darkens it. Stevens found the colour darkened by

* See the observations of E. H. Weber, in Hildebrandt's Anatomie, Bd. iv. p. 491.

† From original researches.

‡ Froriep's Notiz. 759.

sulpho-cyanic acid. Carbonic oxide, carburetted hydrogen, and nitric oxide, are stated by Huenefeld to change it to violet; while nitrous oxide and hydrogen, he says, render it purple, or red brown. I agitated blood with hydrogen gas, but could perceive no change of colour. Berzelius found that the colour of blood, which was already somewhat darkened, was rendered brighter by carburetted hydrogen. It appears, then, that the colour of the blood is changed with great facility by various substances.

Differences between arterial and venous blood.—The specific gravity of arterial and that of venous blood were found by Dr. J. Davy to be very nearly equal,—namely, in the proportion of 1047 to 1050.* According to the same observer, the capacity for caloric of the former as compared with that of the latter, is as 10·11 to 10·10.†

The temperature of arterial blood is stated by Dr. J. Davy to be 1° or $1\frac{1}{2}$° Fahr. higher than that of venous blood.‡ This is confirmed by Krimer and Scudamore; other observers have perceived no difference of temperature.§ Autenrieth, Mayer, Davy, Berthold, and Blundell, agree that arterial blood coagulates more quickly than venous blood; while Thakrah has observed the contrary. Mayer, Blainville, and Denis state, that venous blood yields somewhat less serum and more coagulum than arterial blood.

Arterial blood, according to Mayer's observation, contains more fibrin than venous blood, and yields it in thicker, solid, and shining bundles; in which statement he agrees with Emmert. The results of the experiments of Berthold and Denis, and of one experiment which I performed with the blood of a goat, have been detailed at page 114; and from the mean of these results it appears that arterial contains more fibrin than venous blood in the proportion of 29 to 24. The greater softness of the fibrin obtained from venous, as compared with that from arterial blood, might induce the supposition that the fibrin undergoes some further developement in the respiratory process; but the difference in consistence may be explained by the circumstance that the fibrin in venous blood being in smaller proportion must be in a state of greater division. The smaller proportion of the fibrin in venous blood arises simply from a part of the fibrin being during the passage of the blood through the capillaries appropriated to the nutrition of the tissues; it arises in part, also, from the lymph which contains fibrin in solution being poured into the vascular system near the heart.

It is, however, probable that respiration does contribute to the de-

* See Burdach's Physiol. Bd. iv. p. 381; and Dr. Davy in Phil. Trans. 1814.

† [The experiments in which Dr. Davy himself placed most confidence, afforded 903 and 913 as the numbers indicating the proportional capacity of venous and arterial blood for caloric.]

‡ See page 83.

§ See Burdach's Physiol. iv. 382.

velopement of fibrin, and for these reasons: first, that the blood of the fœtus contains a very small proportion of fibrin, though it is an error to say it contains none; and, secondly, that in the morbus cœruleus, which is dependent on malformations of the heart, such as persistence of the canal in the ductus arteriosus, or of the foramen ovale, tendency to hemorrhage (from deficient coagulability of the blood?) has been observed. The remarkable tendency to hemorrhage from small wounds, which is sometimes witnessed, is, however, an affection distinct from the morbus cœruleus. The assertion of Denis,* that venous blood contains less cruor than arterial blood, appears to me to be merely an hypothesis, for there is no means of estimating the number of red particles in any kind of blood.†

The evidence of different observers respecting the quantity of water in the two kinds of blood is quite contradictory.‡

Abildgaard and Michaelis have made a comparative analysis of arterial and venous blood with reference to their ultimate elements. Abildgaard maintains that venous blood contains less carbon than arterial blood, for it requires one-eleventh or one-tenth less nitre for its complete combustion.§ Michaelis || analysed both kinds of blood by heating them with oxide of copper. The results he obtained are shown in the following table:

	Carbon.	Nitrogen.	Hydrogen.	Oxygen.
Albumen in venous blood . .	52·650	15·505	7·359	24·484
,, arterial blood .	53·009	15·562	6·993	24·436
Cruor in venous blood . .	53·231	17·392	7·711	21·666
,, arterial blood .	51·382	17·253	8·354	23·011
Fibrin in venous blood . .	50·440	17·207	8·228	24·065
,, arterial blood .	51·374	17·587	7·254	23·785

Macaire and Marcet¶ have instituted similar experiments, and obtained similar results.

From these analyses it appears, then, that the cruor of arterial blood contains less carbon than that of venous blood does, which would agree very well with the theory of the excretion of carbon in the form of carbonic acid by the lungs. Again, arterial blood contains more oxygen than venous blood; and this fact would seem to be in favour of the absorption of oxygen by the blood in the lungs. No value, however, can be set upon these facts till they have been found by repeated analyses to be constant, for a slight difference in the drying of the substances to be analysed may make a great difference in the results.

The halitus of the blood seems to be an important part of this

* Rech. exp. sur le Sang Humain. Paris, 1830.

† See page 114.

‡ For an account of the different statements, see Burdach's Physiol. Bd. iv. 383.

§ Pfaff, Nord. Arch. i. 493.

|| Schweigger's Journ. 54.

¶ Ann. de Chim. et Phys. t. li. p. 382.

fluid. But it is not known whether it differs in arterial and venous blood.

Cause of the changes of colour which the blood undergoes.—Arterial blood acquires a dark colour while passing through the capillaries of the body, and its bright colour is again restored in the capillaries of the lungs. If, however, respiration is interrupted, the blood returns from the lungs with its dark venous colour unchanged; while, even after the death of an animal, if respiration is kept up artificially, the change in the colour of the blood in the lungs takes place as before. Division of the nervi vagi does not interrupt the process; indeed blood out of the body is, it is well known, reddened by mere exposure to the atmosphere; and if oxygen is injected into the veins of an animal, even the venous blood of the body becomes of a bright colour.

The study of the causes of these changes will lead us to the theory of respiration, and to the decision of the question, whether the carbonic acid expired during respiration existed previously in the blood, or whether it is formed by the union of the carbon of the blood with the oxygen of the air in the lungs.

The facts relative to this subject which have been ascertained by experiment, may be stated as follows:

1. *The colour of venous blood is not rendered perceptibly brighter by exposure to the vacuum of the air-pump.*—I could perceive no change to a brighter colour in perfectly fresh and still fluid venous blood when it was exposed to the vacuum of the air-pump. Professor Magnus,* however, has observed that a slight change of colour takes place in the blood, if the exhaustion of the air is continued longer, although even then it does not become of so bright a red as arterial blood. The change of the colour of the blood in respiration cannot, therefore, depend on the exhalation of carbonic acid which previously existed in the venous blood; it is most probably owing to oxygen being absorbed.

2. *Blood artificially impregnated with carbonic acid also does not become of a bright colour when exposed to the vacuum of an air-pump.*—I poured about an ounce of bullock's blood, which had been collected half an hour previously when the animal was killed, and which I had freed from fibrin, into a narrow-necked bottle filled with carbonic acid, closed the bottle as tightly as possible, and agitated the blood and gas together. The blood soon became of a perfectly dark violet-red colour. I then exposed some of it in a watch-glass to the vacuum of the air-pump, but perceived no further change in its colour.

3. *Blood impregnated artificially with carbonic acid, and thus darkened, recovers its natural colour in some degree when exposed to the air.*—This I observed when performing the last experiment. It appears, therefore, pretty certain, that the arterialisation of the blood in the air

* Poggendorf's Annal. xl. 602.

and by respiration, does not depend on the removal of carbonic acid from the blood, but on the action of oxygen on the blood.

4. *Blood which has been rendered of quite a dark violet colour by being impregnated with carbonic acid, acquires a bright red colour when agitated with oxygen.*—I had prepared two bottles, one filled with carbonic acid, the other with oxygen. In the first I poured some bullock's blood, and shook it till it was become of a dark violet colour, and then allowed it to stand for some time. I afterwards poured it into the bottle filled with oxygen, closed the bottle quickly, and agitated the blood with the oxygen, when it very quickly became of nearly as bright a red as arterial blood.

5. *The oxygen in which blood impregnated with carbonic acid has been thus agitated, is afterwards found to contain carbonic acid mixed with it.* —At the termination of the last-mentioned experiment, I opened the bottle under water, and endeavoured to remove the blood from the bottle by dilution, adding constantly more water for that purpose, without letting the gas escape; and then, having closed the orifice of the bottle, I removed it, and placed it inverted in a vessel containing lime-water. The lime-water immediately became turbid, and a part of the gas in the bottle was absorbed.

6. *Carbonic acid is evolved likewise when fresh blood is agitated with atmospheric air.*—This has been proved by the experiments of Berthollet,* Christison,† and myself. By agitating seven cubic inches of blood with ten cubic inches of atmospheric air frequently during the space of six hours, I obtained half a cubic inch of carbonic acid gas.‡

7. *No carbonic acid can be obtained from venous blood by the agency of heat.*—Sir H. Davy§ observed an exhalation of carbonic acid both from arterial and venous blood; from twelve cubic inches of arterial blood he obtained 1·1 cubic inch of carbonic acid. The experiment with venous blood consisted in filling a small sheep's bladder with human venous blood, immersing it in water of the temperature of 112° Fahr. and receiving the gas developed in a pneumatic apparatus. The gas consisted of carbonic acid and watery vapour. Dr. John Davy, Strohmeyer, and Bergemann, with myself, on the other hand, failed to detect any evolution of gas when venous blood was heated. In the experiments of Professor Bergemann and myself, one pound of blood was heated to 167° Fahr. even to $189\frac{1}{2}$° and 200° Fahr., but not more than $\frac{6}{32}$ of a cubic inch of carbonic acid was given out. Professor Magnus has shown the reason why carbonic acid cannot be obtained in any perceptible quantity from the blood in this manner. The temperature at which blood re-

* Schweigger's Journal, i. 181.

† Froriep's Notizen, 644. Ed. Med. Journ. vol. xxxv.

‡ An account of these experiments was given in the former editions of this work.

§ Gilbert's Annalen. xii. 594.

mains fluid, is, in fact, too low to set free the carbonic acid; a higher degree of heat coagulates the albumen of the blood; and if albumen previously impregnated with carbonic acid is made to coagulate, the gas cannot be separated from it again by means of heat.

8. *Carbonic acid is set free when venous blood is submitted to the vacuum of the air-pump, or when hydrogen or nitrogen are passed through it.* —Vogel* observed that, when blood was exposed to a vacuum a foam arose, and that the gas being passed through lime-water gave rise to the formation of a small quantity of carbonate of lime. Brande† also detected the presence of carbonic acid in both arterial and venous blood; from an ounce of venous blood he extracted two cubic inches of carbonic acid. Home and Bauer‡ confirmed the observation; they found that carbonate of baryta was formed when a solution of baryta was exposed together with some blood to the vacuum of the air-pump. Sir C. Scudamore§ also had found that blood gives out carbonic acid. And more recently, Dr. Reid Clanny|| obtained one cubic inch of carbonic acid from sixteen ounces of blood.

Dr. J. Davy, on the other hand, obtained the very opposite results. In his experiments fresh blood yielded not a trace of carbonic acid, either in a vacuum, or when heated till coagulation took place: on the contrary, he stated that blood absorbs carbonic acid to the amount of more than a fourth of its volume, and that the gas unites with the alkali of the blood and cannot be separated from it again by a temperature of 200° Fahr. The absorption of carbonic acid by the blood has been confirmed by Mitscherlich, and by Tiedemann and Gmelin.¶

Experiments have been performed likewise by Strohmeyer,** Tiedemann, Gmelin, Mitscherlich,†† and myself,‡‡ with the view of ascertaining whether carbonic acid is exhaled by blood in the vacuum of an air-pump, and all failed to perceive such exhalation.

To the above facts are opposed the experiments of Hoffmann§§ and Stevens,|||| who found that, although no carbonic acid can be extracted from the blood by mere exposure to a vacuum, or heat, yet carbonic acid is evolved when the blood is agitated with another gas, — for instance, hydrogen.

The observations of Stevens and Hoffmann have recently been confirmed by various experimenters. Bertuch and Magnus had satisfied themselves of their correctness some time since; and I have detailed the

* Schweigger's Journ. xi. 401. 207. † Ann. de Chim. et de Phys. x.
‡ Phil. Transact. 1818. 172. Ibid. 1820. § Essay on the Blood. London, 1824.
|| Lancet, Sept. 1834. Müller's Archiv. 1835, p. 120.
¶ See the Journ. de Chim. Méd. v. 246. Jahresb. von Berzelius, x. 233. Froriep's Not. xxi. 209. Tiedemann's Zeitschrift f. Physiol. 5. ** Schweigger's Journal, 1831.
†† Zeitschrift für Physiol. 5. ‡‡ See the former editions of this work.
§§ Med. Gazette, 1833. |||| Ibid. 1834.—Phil. Transact. 1834.

results of their experiments in the Archiv. für Anat. und Physiologie, 1836, p. cxxvii. Bischoff* has obtained the same result from some very accurate experiments. Gmelin also has convinced himself of the existence of carbonic acid in the blood. The experiments of all these observers tend to prove that hydrogen as well as nitrogen, when made to pass through venous blood, become impregnated with carbonic acid gas; and in a proportion as considerable, according to Professor Magnus, as that in which the latter gas is extracted by atmospheric air.

The quantity of carbonic acid taken up by hydrogen gas amounts to at least $\frac{1}{6}$ of the volume of the blood. Bischoff succeeded likewise in producing an evolution of carbonic acid from the blood by means of the air-pump, but in very small quantity. Magnus has found in repeated experiments that a perceptible quantity of carbonic acid is not given out until the air in which it is placed is so rarefied that it supports only one inch of mercury; and this explains why former observers had obtained an opposite result.

9. *A certain quantity of gas can be extracted from arterial blood likewise by means of the air-pump, although none, that can be detected, is given out under the influence of heat.*—Sir H. Davy stated, in the year 1799,† that twelve ounces of the arterial blood of the calf, when heated for an hour to 96°, 108°, and 200° Fahr., yielded him 1·8 cubic inches of gas, of which 1·1 cubic inch was carbonic acid, 0·7 cubic inch oxygen. By means of the air-pump Collard de Martigny obtained from arterial blood carbonic acid, but no oxygen.

Having deprived some arterial blood of the goat of its fibrin by means of stirring, I filled with it a wide glass tube closed at one end, and of a capacity of twelve cubic inches, inverted it in mercury, and heated the apparatus by means of water to $144\frac{1}{2}$°, or 149° Fahr., and kept it at that temperature during several hours; but very little gas was evolved, —namely, not $\frac{1}{16}$ of a cubic inch, and of this phosphorus absorbed $\frac{1}{4}$, or $\frac{1}{5}$.

Magnus ascertained that in a vacuum, arterial blood gives out a considerable quantity of gaseous matter, not less, in fact, than is evolved by venous blood.

10. *Both kinds of blood contain carbonic acid gas, nitrogen and oxygen, but in different proportion; the venous blood contains the most carbonic acid, the arterial blood the most oxygen; the proportion of nitrogen in the two is not always different.*— This important result, which is decisive as to the theory of respiration has been brought to light by the careful and accurate experiments of Magnus. The following table shows the results which he has obtained.

* Commentatio de nov. quibusd. Experim. Chemico-physiol. ad illustr. theoriam de Respiratione institutis. Heidelb. 1837. † Gilbert's Annal. xii. 593.

	Volumes in cubic centimeters.*		of gas	
Blood of a horse	125	yielded	9·8	5·4 Carbonic acid. 1·9 Oxygen. 2·5 Nitrogen.
Venous blood of a horse	205	"	12·2	8·8 Carbonic acid. 2·3 Oxygen. 1·1 Nitrogen.
The same kind of blood	195	"	14·2	10·0 Carbonic acid. 2·5 Oxygen. 1·7 Nitrogen.
Arterial blood of a horse	130	"	16·3	10·7 Carbonic acid. 4·1 Oxygen. 1·5 Nitrogen.
The same blood	122	"	10·2	7.0 Carbonic acid. 2·2 Oxygen. 1·0 Nitrogen.
Venous blood of the same animal	170	"	18·9	12·4 Carbonic acid. 2·5 Oxygen. 4·0 Nitrogen.
Arterial blood of the calf	123	"	14·5	9·4 Carbonic acid. 3·5 Oxygen. 1·6 Nitrogen.
The same kind of blood	108	"	12·6	7·0 Carbonic acid. 3·0 Oxygen. 2·6 Nitrogen.
Venous blood of the same calf	153	"	13·3	10·2 Carbonic acid. 1·8 Oxygen. 1·3 Nitrogen.
The same kind of blood	140	"	7·7	6·1 Carbonic acid. 1·0 Oxygen. 0·6 Nitrogen.

From the above table, it appears that the quantity of gas contained in the blood amounts on the average to $\frac{1}{10}$th, and sometimes is as much as $\frac{1}{8}$th of the volume of the blood itself; that the oxygen in the venous equals at most $\frac{1}{4}$th, and often only $\frac{1}{5}$th of the carbonic acid which the blood contains; while in arterial blood the oxygen equals at least $\frac{1}{3}$rd and almost $\frac{1}{2}$ of the quantity of the carbonic acid.

It must not be imagined, however, that these gases exist in the blood in an aeriform state; they are in a state of solution in it, just as the oxygen and nitrogen in the water of rivers and lakes.

It is only a matter of supposition, arising from the changes which the blood undergoes, that the gases combine more especially with the red particles than with the fluid part of the blood. The red particles are constantly acquiring a bright scarlet colour in the lungs, and resuming their dark red colour in the capillaries of the rest of the body. It is possible that they are the means of communicating the chemical changes which the blood undergoes in the lungs to the other organs of the body.

I have convinced myself by careful observation that in the frog the red particles do not differ in the slightest degree in the arterial and venous blood.

* [A cubic centimeter equals 6·10 cubic inches English].

11. *No carbonic acid is evolved during the change of the colour of venous to that of arterial blood, which is produced by the admixture of neutral salts.*—I filled a graduated cylinder with bullock's blood, from which I had removed the fibrin, added a considerable quantity of nitre, and inverted the cylinder in a vessel which also contained bullock's blood. I then heated the whole apparatus, but no gas was developed.

Dr. Stevens* has made some interesting observations on the share which the salts of the blood have in producing its red colour.

12. *The red coagulum of blood, when placed in distilled water, assumes a darker, in fact, a blackish colour.*—Stevens found that a coagulum placed in distilled water, which extracts the salts, becomes dark, and recovers its scarlet colour on being immersed in a saline solution. Dr. R. Froriep† has confirmed this experiment. It succeeds in a vacuum as well as in the open air.‡ From this fact Stevens draws the inference that it is not the oxygen of the atmosphere, but the serum with its salts, which produces the bright colour of the blood; and that it is for this reason that when the proportion of the salts in the blood is diminished, as in yellow fever and cholera, the blood is darker in colour, and does not acquire the arterial tint when exposed to the air, while it assumes it immediately on salts being added. Hence Dr. Stevens infers that the natural colour of the cruorin is dark or blackish, and that it is red only while in contact with the serum; therefore a coagulum which has been immersed in distilled water, cannot, when exposed to the air, acquire the bright scarlet colour until dipped in a saline solution. The dark colour of venous blood is ascribed, by Dr. Stevens, to the carbonic acid which it is supposed to contain. If this supposition was correct, venous blood ought to become arterial under the air-pump, which is not the case, and also when exposed to hydrogen, for that gas allows of the exhalation of carbonic acid,—indeed, a bladder filled with hydrogen, and placed in carbonic acid, becomes distended to bursting.§ Without denying the necessity of the salts to the production of the arterial colour, it must, however, be confessed, that when oxygen acts on the red particles of the blood surrounded by the saline serum, it gives rise to a brighter colour, without the proportion of the saline matter in the blood being altered.||

* On the Blood, London, 1832.

† Froriep's Not. 759.

‡ Müller's Archiv. 1835. 119.

§ See page 245.

|| See Bischoff, loc. cit.

CHAPTER V.

OF THE CHEMICAL PROCESS OF RESPIRATION.

Conditions on which the process depends.— It would be a great error to suppose that it is only during inspiration that the oxygen of the air permeates the parietes of the air-cells, and the capillary vessels, to enter the blood, and that during expiration the carbonic acid is exhaled through the membranes from the blood. The absorption of oxygen into the blood which is circulating in the capillaries of the air-cells, and the exhalation of carbonic acid from the same blood, goes on uninterruptedly. The acts of inspiration and expiration have no correspondence with the chemical process; they are merely alternate motions of contraction and dilatation of the thorax and of the lungs, which, however, are themselves never completely empty; they always contain some air, which consists partly of atmospheric air, from which the oxygen is being constantly absorbed, and partly of carbonic acid, which is being as constantly exhaled. By the act of expiration the greater part only, not all the air chemically changed by the respiratory process, is expelled: by inspiration a supply of fresh air is drawn into the lungs.

In many animals the respiratory movements of the organs of respiration do not exist, and the constant chemical change only takes place; this is the case in the larva of the salamander, which breathes with external immoveable branchiæ.

It is unnecessary to enter here into any explanation of the property by which the parietes of the air-cells of the lungs allow the oxygen of the atmosphere and the carbonic acid to pass through them,—the former to enter the blood, and the latter to be exhaled. The property of permeability to liquid and gasiform fluids has been shown, in the former book,* to be possessed by all soft animal tissues, particularly by membranes. The process—endosmose or imbibition—must go on with extraordinary rapidity through the delicate parietes of the air-cells of the lungs, and the blood circulating in the membrane forming the cells must participate in the process. Besides, the blood, or rather the red particles, have a remarkably strong affinity for oxygen; hence the rapidity with which venous blood out of the body acquires, when exposed to the air, an arterial colour; carbonic acid being at the same time exhaled. The constant change of dark to bright scarlet-coloured blood goes on in the lungs even after the pulmonary nerves—the nervi vagi—have been divided.

The distribution of the blood in such innumerable capillary vessels

* See page 242.

† Berzelius, Traité de Chimie, t. vii. p. 94.

in the parietes of the air-cells, is then evidently intended to expose it more completely to the action of the air; the whole mass of blood sent to the lungs being, by this means, made to circulate on the vast surface of contact afforded by the air-cells. It is still uncertain whether the pulmonary tissue is endowed in a greater degree than other parts with a specific power of effecting a chemical change in atmospheric air; for the red particles, themselves, seem to act the main part in producing this change in the air, and similar changes take place on other surfaces of the animal body, as on the skin of fishes and frogs, and in the intestines of the cobitis fossilis; moreover, the chemical process of respiration is not arrested by division of the pulmonary nerves. And I have found that frogs will live thirty hours after their lungs have been removed, respiring by means of their skin; while, if immersed in water from which the air has been expelled by boiling, they die much sooner. The lungs are, by virtue of their organisation, by the delicacy of the membrane lining their cells, and the immense surface of contact afforded by them, better adapted than any other parts for the performance of the chemical function of respiration.

Different *theories* have been advanced *to explain the chemical changes effected in respiration.*

1. According to the hypothesis of Lavoisier, Laplace, and Prout, the blood is constantly pouring into the air-cells, by exhalation, a fluid consisting chiefly of carbon and hydrogen, the union of which with the oxygen of the atmosphere gives rise to the carbonic acid and water that are expelled from the lungs by expiration. The existence of the fluid, consisting of carbon and hydrogen, appears to be, in a chemical point of view, quite hypothetical.* Those who adopt this theory, suppose the production of animal heat to depend on the formation of carbonic acid and water in the cavity of the air-cells, not in the blood; it is necessary, therefore, to remark that the temperature of the lungs is generally not at all higher than that of other parts of the body.

2. The theory adopted by most chemists is that of Sir H. Davy, viz. that the air permeates the membranous walls of the air-cells, enters the blood, and in it becomes decomposed in consequence of the affinity of the oxygen for the red particles, carbonic acid being formed, which escapes, in the gaseous form, with the greater part of the nitrogen. Sir H. Davy inferred, from the results of his experiments on the respiration of nitrous oxide and hydrogen, that a certain portion of the carbonic acid produced in respiration is evolved from the blood itself. According to this theory, the animal heat is supposed to be generated in the blood which is circulating through the lungs. The observation of

* See Gmelin's Chemie, iv. 1529.

Dr. J. Davy, that the blood of the left cavities of the heart and of the arteries—the carotid—is warmer by 1°, or $1\frac{1}{2}$°, Fahr. than the blood of the right cavities or veins—the jugular vein—is favourable to this theory.

3. Some physiologists, availing themselves of the fact that during respiration more oxygen disappears than is necessary for the production of the carbonic acid which replaces it, admit that the carbonic acid is formed in the lungs, or in the vessels of the lungs, by the direct combination of a part of the oxygen of the air with carbon of the blood, but suppose that the portion of the oxygen which does not go to form the carbonic acid, does not unite with hydrogen to form water, but becomes chemically combined with the blood, giving to it the arterial colour; and that the red particles thus oxydised form the vital excitants of the tissues of the body. The fact of more oxygen disappearing than is accounted for by the carbonic acid formed, does not justify the assumption of Lavoisier, Laplace, Dulong, and Despretz, that this portion of oxygen which is lost, goes to form the watery vapour, by combining with the hydrogen of the blood. The hypothesis, that the watery vapour exhaled from the lungs is formed in them by the direct combination of its elements, is quite gratuitous; for under the existing external conditions water must evaporate from moist animal surfaces, particularly at the temperature of warm-blooded animals. The hypothesis of the generation of water in the lungs has, therefore, been merely invented to support their theory of combustion, but is not founded on any proofs. The experiments of Collard de Martigny showed that the watery vapour is always exhaled, whatever may be the gas respired; that it continues to be exhaled even in hydrogen gas, when, consequently, no oxygen is present to form it. This fact, however, is, in my opinion, not quite decisive of the question, because animals, when placed in these irrespirable gases, have always some atmospheric air in their lungs. Magendie* states that the exhalation of water from the lungs is increased when water, of the temperature of the body, is injected into the veins. The exhalation of water from the lungs, like the transpiration from the skin, must then be regarded as a simple exhalation from the blood,—not, however, as a mere physical evaporation.† Since it is certain, then, that no formation of water directly from its elements takes place in the lungs, and since most experimenters on respiration, both in air and water, agree that more oxygen disappears than enters into the composition of the carbonic acid which is formed, the excess of oxygen absorbed must unite with the blood, and thus, probably, gives rise to the

* Précis Element. de Physiol. 2nd edit. ii. 246. Translation by Dr. Milligan, p. 453.

† See the remarks on the cutaneous exhalation, in the 8th chapter of the fourth section of this book.

bright colour of arterial blood, and of blood exposed to the air. It is already known that a mixture of red particles and serum, or blood deprived of its fibrin by stirring, is rendered, throughout, of this bright colour by merely passing oxygen through it. The probability of the oxygen combining with the blood is strengthened by the observation, that when blood and air are agitated together, the volume of the oxygen which is absorbed much exceeds that of the carbonic acid formed. The experiments performed by Nysten,* which consisted in injecting gases into the veins of animals, and in which oxygen imparted the arterial colour to the venous blood, of course without any carbonic acid being evolved, are also in favour of this opinion.

4. According to the theory of Lagrange and Hassenfratz, the oxygen absorbed into the blood, in which it is merely in a state of solution, or combined in some way with the red particles, does not unite in the lungs with the carbon of the blood; they suppose the combination to be accomplished in the course of the circulation, carbonic acid thus formed being retained in the blood, until, reaching the lungs, it is set free. Lagrange founded this opinion partly on the fact that arterial blood, contained in close vessels, assumes spontaneously, after a time, a dark colour. Now since arterial blood does not lose its bright colour and become venous until it passes through the capillaries, the formation of carbonic acid, supposing the theory of Lagrange to be correct, can take place only in the capillary vessels of the body. In that case the venous blood ought to contain principally carbonic acid in solution, the arterial blood oxygen in some way loosely combined. This view of the respiratory process has been adopted by a great number of physiologists, and was chiefly supported by the experiments of Vogel, Home, Brande, Scudamore, and Collard de Martigny, which seemed to prove that venous blood really contains carbonic acid; and by the experiment of Sir H. Davy, from which he concluded that oxygen can be obtained from arterial blood by heat. It explains why the lungs are not warmer than other parts of the body. F. Nasse has, in an excellent treatise on respiration,† collected all the earlier facts supporting this theory. Experiments which yielded contrary results, and which we have already detailed, had thrown a doubt on the correctness of this view. But the observations of Stevens, Hoffmann, Bischoff and Bertuch, who have shown that venous blood contains carbonic acid, and still more those of Magnus, who has demonstrated the existence of gas and its composition in both kinds of blood, have rendered this theory the most probable.

5. Dr. Stevens has recently advanced a new theory of the respiratory process, which at first view appears ingenious. According to Stevens, the colouring matter of the blood is itself dark, but is rendered

* Rech. de Physiol. et de Chim. Pathol.

† Meckel's Archiv. ii. 195, 435.

scarlet by the salts of the serum. The natural colour of the blood, therefore, as long as it is in contact with serum, is bright red or scarlet; but if the coagulum of blood is dipped in water, the red colour becomes dark, on account of the serum with its salts being washed out of the coagulum by the water. The blood, naturally of a bright colour, is rendered dark by carbonic acid. Carbonic acid, Stevens says, is formed in the capillaries, hence the dark colour of venous blood; it is excreted in the lungs, and the natural bright red colour of the blood is thus restored, the oxygen having no share in producing the change of colour. If Dr. Stevens's theory was correct, venous blood ought to become of a bright colour in the vacuum of an air-pump, from the escape of the carbonic acid; this, however, as we have already seen, does not take place. The oxygen, therefore, which is absorbed by the blood in the lungs must be the essential cause of its arterial colour. De Maack,* states that the red colouring of the blood is of a blackish colour, as well when it is impregnated with oxygen, as when it contains more carbonic acid, as long as it does not come into contact with a solution of neutral salts. Salts render cruor of both kinds red,—the first of an arterial hue, the latter of the venous tint. De Maack confirms the observation of Berzelius, that serum absorbs only an extremely small quantity of oxygen, and evolves no carbonic acid. A solution of red colouring matter, on the contrary, measuring two and a half volumes, absorbed from two volumes of oxygen one and a half volume, and afterwards, on a saline fluid being added, became of a bright red colour. De Maack imagines that the colouring matter which is impregnated with carbonic acid, is decomposed by oxygen, the colouring matter becoming oxydised while the carbonic acid is set free; just as carbonate of the protoxide of iron undergoes decomposition in moist air, being converted into hydrate of the peroxide.

6. According to another theory of the respiratory process, the carbonic acid cannot be generated by the union of the oxygen of the air with carbon of the blood, because the exhalation of carbonic acid goes on when gases containing no oxygen are respired; it is supposed therefore to be formed from the ultimate elements of the blood, like other secretions. The secretion of different gases by the air-bladder of fishes may be adduced in support of this hypothesis, which, if correct, would lead to the inference that the carbonic acid would not necessarily exist already formed in the venous blood, but might be generated in the capillaries of the lungs independently of the concurrent action of oxygen. This theory rests on the statement that cold-blooded animals continue to exhale carbonic acid even when made to respire in gases which contain no oxygen, which was the result of experiments made originally by Spallanzani, and since repeated by Edwards. The existence of the gases in the blood itself,

* De ratione quæ colorem Sanguin. inter et Respirationis functionem intercedit. Kil. 1834.

however, proves that they are not the product of a secreting action of the lungs.

7. Mitscherlich, Gmelin, and Tiedemann have lately proposed a perfectly original theory of respiration. The facts on which they ground their opinion are the following: that acetic and lactic acid exist in the free or combined state in most secretions, and also in the blood; and these acids, they say, must be generated in the animal body itself, because they are contained in much smaller quantity in the food than in the cutaneous and renal secretions by which they are being constantly eliminated from the body. They have further ascertained that venous blood contains more alkaline sub-carbonates than arterial blood: 100 parts of venous blood containing, at least, 12·3 parts of combined carbonate of an alkali; arterial blood, at least, 8·3 parts. They suppose now that by the free contact of the blood with the air during respiration acetic acid is generated, which decomposes the alkaline carbonate of the venous blood, and sets free the carbonic acid,—that the oxygen of the inspired air, namely, unites, in part, directly with carbon and hydrogen, and forms carbonic acid and water, and in part enters into combination with the organic compounds contained in the blood; the result of which is that organic products which are necessary to life are produced; and, at the same time, other organic substances are converted into lower organic products, such as the acetic and lactic acids, which decompose a part of the carbonates contained in the blood, and expel the carbonic acid into the air-cells of the lungs.*

While the existence of gases in the blood itself was doubtful, this was an ingenious mode of explaining the phenomena; but Gmelin himself has since recognised the existence of carbonic acid in the blood.

In determining the nature of the chemical process of respiration, all depends on the solutions afforded to the following questions:

1. Does venous blood contain carbonic acid, and arterial blood oxygen? This question has been determined in the affirmative by experiments which we have already mentioned, particularly the excellent researches of Magnus.

2. Is the carbonic acid contained in the blood extracted from it by other gases as well as by atmospheric air? The experiments of Hoffmann, Stevens, Bischoff, Bertuch, and Magnus have shown that this likewise is the case. Hydrogen and nitrogen, brought freely in contact with blood, become impregnated with carbonic acid in as large proportion as atmospheric air which has been passed through that fluid.

3. Is carbonic acid exhaled from the lungs of cold-blooded animals in an atmosphere of pure hydrogen or pure nitrogen? We shall see that this is most certainly the case.

Products of respiration in hydrogen and nitrogen.—I will now give an

* Tiedemann's Zeitschrift f. Physiol. 5.

account of the whole series of experiments relative to the exhalation of carbonic acid during respiration in gases which contain no oxygen. The earlier experiments of Sir H. Davy,* Coutanceau, and Nysten,† having been instituted on warm-blooded animals, are of no value, for the lungs of such animals, which can be kept in hydrogen but a short time, contain carbonic acid at the commencement of the experiment. No certain conclusions can be drawn from the experiments unless the animals are kept for a considerable time in the hydrogen or nitrogen, and unless the quantity of carbonic acid formed is large. M. Edwards‡ obtained such a result; a frog, being kept eight and a half hours in hydrogen, afforded by respiration 2·97 centilitres, or 1·80 cubic inch English, of carbonic acid; a result in which, however, there must have been some error, for even in atmospheric air a frog does not generate nearly so much carbonic acid in that period of time. Collard de Martigny§ performed a similar experiment with nitrogen, and also observed the generation of carbonic acid in a quantity not much less than that which Edwards mentions. He removed the frog from the jar of nitrogen at intervals of from one and a half to two hours, and, by a particular apparatus, collected the gas in another vessel; he then filled the jar again with nitrogen and replaced the frog in it. This he repeated several times in each experiment. Before placing the frog in the gas, the lungs and throat were always compressed. This method has some advantages, but the repeated removal of the frog might lead to error; for, each time that the animal was replaced in the gas, a small quantity of atmospheric air must have been introduced with it by means of the respiratory organs, however closely they might be compressed. Collard has not mentioned how he prepared and purified the nitrogen. The results of his experiments are shown in the following table:

Experiments.	*Number of Frogs.*	*Duration of Experiment.* H.	M.	*Volume of Carbonic found.* Centil.	*Volume for one Frog in cubic Inches, English.*
A	1	7	30	2·80	1·70
B	3	8	0	7·98	1·61
C	2	8	30	5·22	1·58
D	2	8	0	5·43	1·64
E	2	7	30	4·89	1·47
F	2	9	0	5·15	1·55
G	2	8	40	5·70	1·72

I thought it very requisite to repeat these experiments of Edwards and Collard, and, having twenty pounds of mercury at my disposal, I was

* Gilbert's Annal. xix. 320. † Meckel's Archiv. ii. 256.

‡ Infl. des Agens Phys. p. 445. Dr. Hodgkin's Translation, p. 236.

§ Magendie's Journal, 1830, p. 121.

enabled to perform them on a large scale.* I have arranged the results which I obtained, together with those of some experiments by Professor

* Experiment A.—A cylinder, of the capacity of twenty cubic inches French, [about twenty-four cubic inches English,] filled with and inverted in mercury in the usual manner, was filled with hydrogen prepared from zinc and dilute sulphuric acid. Four frogs were introduced into the cylinder with their lungs compressed; at the end of four hours their respiratory movements had ceased, although they still showed signs of life. At the expiration of twelve hours I removed them; they were dead, and did not revive when exposed to the air. Caustic potash introduced into the cylinder absorbed $1\frac{4}{5}$ cubic inch French, of carbonic acid; amounting, for a single frog, to 0·45 cubic inch French [or 0·54 cubic inch English]. In this experiment the hydrogen was impure, in which state it contains fœtid oil and some carbonic acid. (Gmelin's Chemie, i. 217.)

Experiment B.—In another experiment, performed in conjunction with Professor Bergemann, the hydrogen was purified by being passed through alcohol; and a smaller cylinder, of the capacity of ten French cubic inches [twelve English cubic inches], was used. A frog was introduced, and at the end of twelve hours showed feeble signs of life, and breathed at long intervals, and even at the end of twenty-two hours was only in a state of asphyxia; on testing the gas with caustic potash, half a cubic inch French [0·60 of a cubic inch English] was absorbed. The frog revived, and was used by Professor Bergemann in several other experiments, namely, in four experiments with hydrogen and two with nitrogen. After some time it was returned to me, and was then quite lively: its blood coagulated like that of other frogs.

Experiment C.—I kept a frog during four hours in hydrogen, which had been passed through alcohol; at the end of that period it was apparently dead, the heart's pulsation ceased for minutes at a time; but the animal revived when restored to the air. A second frog was now placed in the same cylinder for two hours and a half, at the end of which time it was in appearance dead; on analysing the gas, by means of caustic potash, 0·83 of a cubic inch French [0·99 cubic inch English] of carbonic acid was absorbed. The column of mercury in the barometer measured twenty-nine inches five lines.

Experiment D.—Two frogs were confined for six hours in hydrogen which had been passed through solution of potash; they were torpid at the end of the experiment: carbonic acid to the amount of 0·66 of a cubic inch French [0·79 of a cubic inch English] had been formed. The height of the barometer was 29 inches $8\frac{1}{2}$ lines; the temperature was $65\frac{1}{4}$° Fahr.

Experiment E.—The vessel used for the developement of the hydrogen was always nearly full, so that it contained only very little atmospheric air in the space above the fluid, and a large quantity of gas was always allowed to escape before the hydrogen was collected for the experiment; it was therefore pretty certain that there was no source of error in this part of the experiment. But to remove all suspicion of the presence of oxygen, I introduced a ball of platinum sponge into the hydrogen, which had been previously passed through solution of potash, and left it there for twenty-four hours. I then placed the frog in the cylinder, compressing its lungs at the time, as in the other experiments. In eight hours he was apparently dead. The quantity of carbonic acid formed was 0·4 of a cubic inch French [0·48 of a cubic inch English]. In all the experiments the gases were collected over mercury. I have performed three other experiments; in which, however, I purified the gas by shaking it after it was collected with liq. potassæ. The result of these experiments was perfectly similar to that of the others. In experiment F, 0·37 of a cubic inch [0·44 of a cubic inch English] of carbonic

Bergemann,* in a tabular form. Those of my experiments distinguished by the letters A, F, G, H, (see the note at the preceding page,) not being free from suspicion of error, are not included.

Name of Observer.	*Gas respired.*	*Experiment.*	*Duration of Experiments.* Hours.	*Volume of Carbonic Acid generated.* *in decimals of French cubic Inch.*	*in decimals of English cubic Inch.*
Müller	Nitrogen	A	6	0·25	0·30
Bergemann	Do.	A	14	0·75	0·90
Do.	Do.	B	12	0·5	0·60
Müller and Bergemann	Hydrogen	B	22	0·5	0·60
Müller	Do.	C	$6\frac{1}{2}$	0·83	0·99
Do.	Do.	D	6	0·33	0·39
Do.	Do.	E	8	0·4	0·48
Bergemann	Do.	A	10	0 55	0·66
Do.	Do.	B	12	0·8	0·96
Do.	Do.	C	13	0·7	0·84
Do.	Do.	D	14	0·5	0·60

It might still be objected to these experiments,† that the frogs retained a certain quantity of atmospheric air in their lungs, and that their in-

acid was generated by a frog in twelve hours; in experiment G, 0·41 of a cubic inch [0·49 of an English cubic inch] ; and in experiment H, 0·4 of a cubic inch [0·48 of a cubic inch English] in the same space of time. But I consider the last three experiments as defective, because the water with which I washed out the caustic potash used to purify the hydrogen gas was not boiled, and therefore contained atmospheric air, some of which it might have imparted to the hydrogen.

I placed a frog in nitrogen prepared by the combustion of phosphorus ; it lived six hours, and the carbonic acid formed amounted to a quarter of a cubic inch French [0·30 of a cubic inch English.]

* Professor Bergemann has sent me the following notes of his experiments. They were made with hydrogen and nitrogen, in a room the temperature of which was kept between 41° and $54\frac{1}{2}$° Fahr. The same frog served for all the experiments. An increase in the volume of the gas, which was greatest during the first three hours, was observed both when hydrogen and when nitrogen was respired. After the lapse of four or five hours, the vitality of the frog diminished considerably. The respiration was unequal, and at the end of eight or nine hours ceased during long intervals, but could be re-excited by a slight motion of the cylinder. At the termination of the experiment the frog was always quite torpid, but after a few hours moved more freely, and in a few days could be again employed for a similar purpose. In each experiment *the yellowish colour of the frog changed to a dark brown.* The hydrogen used was prepared from zinc and dilute sulphuric acid, and was purified by means of alcohol. The nitrogen was obtained from the atmosphere by burning a combustible body in it, and was afterwards agitated in lime-water. Small quantities of oxygen, however, always remain in nitrogen thus prepared. The experiments with nitrogen, therefore, cannot lay claim to great exactness. The frog was introduced into the gas with its lungs compressed. The volume of hydrogen and nitrogen used varied from $8\frac{1}{2}$ to $9\frac{2}{3}$ cubic inches English.

† Described in the notes, pages 337 and 338.

testinal canal might also contain carbonic acid. I have, therefore, repeated the experiments in such a manner as to avoid these objections, exposing the frogs first to the vacuum of the air-pump, and then filling the vacuum with hydrogen. In one experiment I even removed this hydrogen again, by means of the pump, so as to free the bell of the air-pump from every portion of atmospheric air. It was also ascertained that the hydrogen, after the watery vapour was removed by means of chloride of calcium, was not diminished in volume by caustic potash. The frogs were left in the hydrogen for the space of three hours, but long before that time had elapsed they were in a state of asphyxia. They were then removed, and the gas freed from watery vapour by means of chloride of calcium; a tube containing that substance being introduced repeatedly during a whole day, until it ceased to gather moisture. The gas was then tested with caustic potash. In both of the two experiments the usual exhalation of carbonic acid was evident; in the first it amounted to 0·3 of a French cubic inch [0·36 of an English cubic inch]; in the second, to 0·37 of a cubic inch French [0·44 of an English cubic inch].

The quantity of carbonic acid, then, which a frog exhales in from six to twelve hours in gases that contain no oxygen, may be safely estimated at from $\frac{1}{4}$ to $\frac{4}{5}$ of a cubic inch French [from $\frac{3}{10}$ths to $\frac{96}{100}$ths of a cubic inch English]. The capacity of the lungs and throat of a frog, on an average, is not more than $\frac{3}{8}$ or $\frac{1}{2}$ of a cubic inch French [$\frac{9}{20}$ths or $\frac{6}{10}$ths of an English cubic inch]; and in these experiments the lungs and throats were both compressed, so that they could not have contained much atmospheric air and carbonic acid, even if a small quantity had remained. The fact, therefore, which Spallanzani ascertained cannot be disputed; cold-blooded animals continue to exhale carbonic acid even in gases which contain no oxygen, and in nearly as large quantity as when respiring atmospheric air; for it appears from experiments detailed at page 311, that the average amount of carbonic acid generated by a frog breathing atmospheric air, is, in six hours, 0·57 of a cubic inch French [0·68 of an English cubic inch].

These results have been recently confirmed by the equally instructive experiments of Bischoff, who likewise found, that after the lungs of frogs had been tied and cut out, carbonic acid (to the amount of 0·20 of a French cubic inch [0·24 of an English cubic inch] in eight hours) continued to be exhaled by the skin.

The fact of the exhalation of carbonic acid by frogs breathing in gases which contain no oxygen was stated, and the above experiments detailed, in the previous editions of this work, but it then appeared that no carbonic acid was contained in the blood itself. Hence, at that time the theory that the carbonic acid expired in respiration is in part a product of secretion, and can be formed independently of atmospheric air, seemed

probable, and the formation of the carbonic acid in the lungs was likened to the process by which in fermentation this gas is generated from the elements of organic substances without the contact of atmospheric air being essential. If the "secretion"-theory, however, were correct, we should expect that the lungs or skin alone would possess the property of exhaling carbonic acid; that this gas would not be generated by simply agitating blood with atmospheric air, which however we showed to be the case. Seven cubic inches of blood agitated almost constantly for six hours with ten cubic inches of atmospheric air yielded half a cubic inch of carbonic acid. Till within the last few years, therefore, the theory of respiration was involved in inexplicable difficulties. Blood agitated with atmospheric air was known to yield carbonic acid without the influence of the living organ, becoming at the same time of a bright red colour; the blood was believed to contain no pre-existing carbonic acid; and yet frogs were found to exhale carbonic acid when no oxygen was respired, and in nearly as large a quantity as in atmospheric air.

Now, however, the problem is satisfactorily solved. The excellent experiments of Professor Magnus have shown that both kinds of blood contain oxygen, nitrogen, and carbonic acid gas, that the arterial blood contains more oxygen than the venous blood, while the carbonic acid is in larger quantity in the venous than in the arterial. During respiration carbonic acid is extracted from the blood by the atmospheric air, oxygen being yielded to the blood in its place; a portion of the carbonic acid still remains, however, dissolved in the arterial blood. In the process which is constantly going on between the blood and the texture of the organs in the capillary vessels of the body, the oxygen, which is a vivifying stimulus for the organised substance, disappears in part from the arterial blood, and carbonic acid is formed, the venous blood therefore contains a large proportion of carbonic acid, but it retains some of the oxygen. The venous blood reaching the lungs is again deprived of a part of its carbonic acid by the action of the atmospheric air. The interchange of the carbonic acid and oxygen in the lungs is wholly in accordance with the physical laws of the absorption of gases. A fluid impregnated with a particular gas does not give it out as long as its surface is subjected to the pressure of the same gas; but if it is brought into contact with a different gas, an interchange takes place until the gas with which the fluid is impregnated, and the gaseous atmosphere which presses upon it, are equally mixed. This law affords a ready explanation for the exhalation of carbonic acid by frogs in hydrogen and nitrogen in as large quantity as in atmospheric air, as well as for the fact that hydrogen and nitrogen transmitted through blood become impregnated with the carbonic acid which it contains.

The proportion of carbonic acid contained in the blood is sufficiently large to account for the whole quantity exhaled from the lungs.

Supposing that two ounces of blood are expelled from the heart at each beat, ten pounds must pass through the lungs in a minute; and these ten pounds of blood ought to contain 27·4 cubic inches of carbonic acid,—such being the volume of this gas which Allen and Pepys found to be exhaled from the lungs during a minute's respiration. But admitting that the quantity of carbonic acid really exhaled from the lungs is one-half less than the experiments of Allen and Pepys would indicate,—and it certainly is less, — and adopting the estimate of Sir H. Davy, who calculated that 15·8 cubic inches is the amount of carbonic acid gas exhaled from the lungs during each minute, still ten pounds of blood ought to contain nearly 16 cubic inches of that gas.

The experiments of Professor Magnus have shown that the blood contains at least one-fifth of its volume of carbonic acid; and since one pound of blood measures about 25 French cubic inches, [one pound avoirdupois of water contains 27·7 English cubic inches, the same weight of blood about 26·4 English cubic inches,] every pound of venous blood ought to contain at least five cubic inches of carbonic acid, and the ten pounds of blood which pass through the lungs in a minute, 50 cubic inches [60 English cubic inches], of which it can easily be conceived that 15·8, or even 27·4 cubic inches, may be exhaled in the respiratory process.

A small quantity of nitrogen is absorbed by the blood from the air respired, but does not appear to perform any office in the system, since its proportion is the same in both arterial and venous blood.

The object which the respiratory process is intended to attain is evidently the absorption of oxygen into the blood, which conveys that gas as a stimulus to the different organs of the body; and, secondly, the removal from the blood of the carbonic acid which is formed in the capillaries. That the latter is not the main object is clearly shown by frogs falling into a state of asphyxia when made to respire in hydrogen and nitrogen, although the quantity of carbonic acid which is exhaled in those gases is not in the slightest degree less than in atmospheric air.

CHAPTER VI.

OF THE RESPIRATORY MOVEMENTS AND THE RESPIRATORY NERVES.

a. The movements of Respiration.

In mammalia generally, as well as in the human subject, inspiration and expiration are performed by the dilatation and contraction of the cavity of the thorax. As soon as the parietes of the thorax are drawn wider asunder and the thorax dilated, the external air rushes through the trachea and its branches into the air-cells, which it distends in proportion to the dilatation of the thorax, thus keeping the surface of the lungs accurately in contact with the thoracic parietes in all their move-

ments. This can only take place, however, while the thoracic cavity is closed on all sides, so that the air cannot exert any pressure on the outer surface of the lungs, by which the pressure of the air entering by the trachea, on the inner surface, would be balanced. In cases of penetrating wounds of the thorax, a full inspiration cannot be performed, because the counter pressure of the air entering by the wound balances the pressure of the air on the inner surface, by which the lungs would otherwise be distended. The lungs in this case remain collapsed, although the thoracic parietes dilate.

Inspiration.—The diaphragm contributes the principal share to the dilatation of the chest during inspiration. In the state of relaxation the diaphragm is arched: by contracting it becomes more plane; and by the flattening of its arch the capacity of the thorax is increased, at the same time that the abdominal viscera are pressed upon from above so as to produce the protrusion or apparent enlargement of the abdomen which is observed during inspiration.

As soon as the diaphragm becomes relaxed, the abdominal viscera recede, and the abdomen again becomes flat. In a natural tranquil inspiration, the dilatation of the chest is effected almost wholly by the diaphragm. The lateral dilatation of the thorax is performed principally by the action of the intercostal muscles, assisted also by the scaleni, levatores costarum, the serratus posticus superior, and the thoracic muscles generally.

Expiration in perfectly tranquil respiration may be the result of the mere collapse or elastic reaction of the parts recovering their natural state after the active dilatations which they have undergone; and, in fact, tranquil respiration seems to consist, not so much of alternate actions of antagonising muscles, as of the periodic action of the muscles of inspiration solely. [The elasticity of the lungs themselves, and the share which they have in producing expiration, have been particularly investigated by Dr. Carson of Liverpool. He made several experiments to determine the force exerted by the lungs by virtue of their elasticity in expelling the air after the act of inspiration had ceased. "In calves, sheep, and large dogs, the resiliency of the lungs was found to be balanced by a column of water varying in height from one foot to a foot and a half; and in rabbits, by a column of water varying in height from six to ten inches."]* The muscles of expiration may, it is true, assist by that passive kind of contraction which all muscles possess in addition to their stronger contractile power. However this may be, expiration ensues spontaneously, as soon as inspiration ceases. During a more forcible expiration the expiratory muscles act more strongly, especially when any irritation is excited in the larynx or lungs, in which case they act even spasmodically so as to produce cough. The

* Phil. Trans. 1820.

muscles of expiration are the abdominal muscles, which draw down the ribs, and by compressing the abdomen force upwards the viscera against the relaxed diaphragm, and thus diminish the capacity of the thorax from below. These muscles are the recti, obliqui, and transversi abdominis, the quadratus lumborum, the musculus serratus posticus inferior, the sacrolumbalis, and the longissimus dorsi.

Expiration is assisted, first, by the elastic contraction of the air tubes after their distension by the air has ceased; secondly, by contraction of muscular fibres of the air tubes.

Motions of the larynx and fauces.—The glottis is dilated during inspiration, and contracted during expiration. The bronchial tubes are also dilated during inspiration, and contracted during expiration. The air enters and is expelled either by the nose or the mouth. When the air is drawn in and expelled by the nostrils only, the passage through the mouth is closed by the posterior part of the tongue being pressed against the palate; if respiration is performed by the mouth, the soft palate is elevated. By approximating the posterior palatine arches, by which means Dzondi* has discovered that the opening from the mouth to the pharynx is completely closed, and by pressing the root of the tongue against the palate the mouth, as well as the nostrils, can be completely cut off from the air tubes. This movement is often performed voluntarily, as in holding the breath, and in arresting the passage of unpleasant odours through the nose.†

Muscular contraction of the lungs and air tubes.—The hypothesis of the lungs themselves aiding in the movements of respiration, has from

* Über die Functionen des weichen Gaumens. Halle, 1831.

† In birds the air during inspiration enters not merely the lungs, but also the great air cells. Birds have no perfect diaphragm; a few muscular bands arising from the posterior angles of the third, fourth, and fifth rib pass upwards to be attached to a fibrous membrane at the under surface of the lungs. The dilatation of the thorax produces dilatation of large intervisceral cells which communicate with the lungs, and the air is thus drawn into the lungs, through which it must pass to reach these cells. The air is expelled again from these cells, and from the lungs, by the action of the abdominal muscles. In the chelonian reptiles the ribs are immoveable, and the amphibia—cœciliæ, derotremata, proteida, and batrachia—have no true ribs; in these classes consequently the air is taken in by movements of deglutition. Frogs, having closed the opening of the mouth, dilate the cavity of the mouth and throat, so as to draw in the air by the nostrils; then closing the internal apertures of the nostrils by a peculiar mechanism, and the pharynx at the same time, they contract the cavities of the mouth and throat so as to force the air through the glottis into the lungs. The air is expelled partly by the action of the abdominal muscles, and partly by the elasticity of the lungs, the glottis being opened. In the tortoise and turtle the expiration is performed by the contraction of the abdominal vessels between the lower shield or plastron and the posterior extremities. The reptiles which have moveable ribs respire by enlarging and diminishing the capacity of their trunk by means of their ribs. For the mechanism of the respiration in fishes, consult Cuvier's Leçons d'Anat. Comp.

the earliest times been alternately adopted and rejected. Averroes, Riolan, Plater, Sennert, and Bremond* were in favour of it. Th. Bartholin, Diemerhoeck, Mayow, and Haller† were opposed to it. The former writers observed that, in animals of which the thorax was laid open during life, the lungs did not always collapse, but in some cases continued to move, although the muscles of the thorax could no longer act. More recently, Flormann and Rudolphi have defended this hypothesis.‡ In a dog which was drowned, the lungs appeared to Flormann to continue to move even after the diaphragm had been divided; and Rudolphi saw the lungs of a dog which had been strangled continue to move even after the sternum had been removed, and the diaphragm and intercostal muscles divided. Such movements have been attributed to shocks communicated from the thoracic parietes; they might also arise from contractions of the heart or of the pulmonary veins. Haller never saw these motions of the lungs; in his experiments the lungs always collapsed perfectly when the thorax was completely opened: the result of my experience is the same, and I conjecture that Flormann and Rudolphi must have been deceived. The further consideration of this controversy is merely of historical interest; arguments and counter-arguments are repeatedly brought forward, and the inquirer is at last left to the testimony of his own eyes, which in my case is opposed to the hypothesis. Motions were observed by Tiedemann in the respiratory organ of the holothuria. Treviranus relates that he has seen motion excited in the lungs of the frog by the application of tincture of opium and extract of belladonna. I do not know whether the celebrated author of the "Biologie" attributes much importance to this observation. Frogs fill their lungs with air from their throat, and the air escapes on the glottis and nostrils being opened. If the glottis is opened, the lungs become permanently collapsed, and no contractions can be excited in them.§

The contractile power of the trachea and its branches is, however, less equivocal. It might be supposed that the bronchi contributed to produce the motions observed by Houstoun, Bremond, Flormann, and Rudolphi. It is, however, still matter of doubt whether the muscular fibres of the trachea produce any *rhythmic* motions of contraction and dilatation. The transverse muscular fibres on the posterior surface of the trachea are well known. Muscular fibres are also described as existing on the smaller bronchi. Reisseissen|| has contributed most to draw attention to these fibres. He says that by means of a lens he has re-

* Mém. de l'Acad. d. Sc. Par. 1739.

† Elementa Physiol. t. iii. l. viii. p. 226.

‡ Rudolphi, Anat. Physiol. Abhandl. p. 111.

§ Consult, on this subject, Lund, Vivisectionen, pp. 243—240.

|| De fabricâ Pulmon. Berol. 1822, fol.

cognised muscular fibres on bronchi so small that the cartilaginous plates were no longer detectible.

It is remarkable that there exists at present no direct proof of the contractility of the muscular fibres of the trachea and its branches. All the ducts of glands possess true muscular contractility, they have the power of involuntary motion.* But contractions of the fibres of the trachea have hitherto been observed by Krimer† only. Wedemeyer applied mechanical stimuli and galvanism to the whole circumference of the trachea in a dog and a hedge-hog, both with and without previous division of the mucous membrane, but could perceive no contractions produced; while bronchi of three-fourths of a line to a line in diameter contracted gradually until their cavity was nearly obliterated. Wedemeyer laid bare the trachea in a living dog, and freed it from cellular tissue for the space of two inches; he then cut out a portion in front, and irritated the posterior wall of the trachea mechanically and by galvanism, but could not produce the slightest contraction. Wedemeyer now opened the thorax quickly, and removed the lungs with their bronchi. He made several sections of the larger bronchi, but could discover no sign of contractility in them. On applying galvanism, however, to the smaller branches of about one line in diameter, he thought that he saw them undergo a distinct constriction, but it took place very slowly. The last phenomenon had been before observed by Varnier. It is probable, therefore, that the bronchial tubes and trachea do not contract and dilate rhythmically during the movements of respiration. Had they this power, it would be quite an isolated fact; for although the hepatic duct presents rhythmic contractions, they are quite independent of the will, while, if the bronchi contracted and dilated synchronously with the other respiratory movements, their action, like that of the other parts engaged in respiration, must also be subject to the will, and it is highly improbable that the branches of the efferent tube of an internal viscus would be thus under the influence of the will. It is possible that the fibres of bronchi may possess a contractile power which is constantly in action, and which may effect the contraction of the tubes on the cessation of the act of inspiration: but mere elasticity would be sufficient for this purpose.

In man the dilatation of the bronchi, and the shortening of the trachea during respiration, and its lengthening during expiration, which some physiologists have observed, seem to be merely the mechanical results of the dilatation and contraction of the thorax; the larynx itself descends a little during violent inspiration, and ascends again during expiration.‡

* See section on Secretion.

† Untersuchungen über die nächste Ursache des Hustens. Leipz. 1819.

‡ Birds have certainly the power of shortening their trachea by means of particular

b. Of the influence of the nerves on the function of respiration.

The source of the nervous influence on which the respiratory movements depend is one and the same, although the nerves implicated in these movements are very various.

The respiratory movements are: 1st. Movements in the face, which, however, are but seldom exerted in rhythmic order; such are the elevation and depression of the alæ of the nose, and the straining of several muscles of the face during respiration. These movements are observed in violent involuntary acts of respiration, and even in a state of great debility; they are under the influence of the facial nerve, which Sir C. Bell calls the respiratory nerve of the face. 2nd. Dilatation of the glottis during inspiration, and its contraction during expiration. This motion is wholly subject to the action of the two laryngeal branches of the nervus vagus, the nervus laryngeus superior et inferior seu recurrens. 3rd. Lateral dilatation of the thorax during inspiration, effected through the agency of the spinal nerves, the nervus respiratorius externus of Bell, and the nervus accessorius Willisii which supplies the trapezius with nervous influence for the elevation of the shoulder. 4th. Contraction of the diaphragm in the act of inspiration, —the phrenic nerve. 5th, and lastly, contraction of the abdominal muscles in expiration,—nervi spinales. The respiratory nerves, then, are the portio dura of the seventh, the nervus vagus, nervus accessorius, and many spinal nerves distributed to the muscles of the trunk.

Each of these nerves has its own sphere of action, and one of them may be deprived of its function without the others being affected. The division of any one of them puts a stop to that set of movements which depend upon its influence; but destruction of the medulla oblongata annihilates all the respiratory movements, and the action of all those nerves which arise from the spinal cord. The medulla oblongata is the source from which the nervous influence for the respiratory motions is derived; and the spinal cord is, at it were, the trunk of the nerves which arise from it. If the spinal cord is divided above the point where the dorsal nerves are given off, the motions of the ribs and abdominal muscles are paralysed: the other respiratory movements con-

muscles, the musculi sterno-tracheales and ypsilo-tracheal; and in many birds there are several muscles at the inferior larynx at the division of the trachea for the purpose of producing their song. It is a very interesting fact, that the former muscles are supplied with a special nerve, and a second descending branch of the ninth nerve, which descends as far as the inferior larynx, and (in the turkey) supplies the muscular sterno and ypsilar tracheals, while the recurrent nerve, destined chiefly for the œsophagus, gives a proportionally short branch to the trachea. I have hitherto had no opportunity of ascertaining the correctness of the assertion of Desmoulin, that the inferior larynx is supplied from the inferior cervical nerves.

tinue. If the spinal cord is cut through above the origin of the phrenic nerves, the diaphragm is paralysed, while the nerves given off from the medulla oblongata itself still continue to exert their function. The nerves coming off from the spinal cord below the lesion are still capable of exciting motions when irritated singly, but they can no longer receive the motor influence from the common source of all the simultaneous, voluntary, and involuntary movements of respiration. Injury of the medulla oblongata puts an end immediately to all the respiratory motions, as well to those dependent on the nervus vagus as to those of the trunk, which are dependent on spinal nerves.

Legallois pointed out this connection between the medulla oblongata and respiration; he proved that no other parts of the brain are the source of the respiratory movements, and that the brain of an animal may be removed piece by piece from before backwards, until, on wounding the medulla oblongata at a point corresponding to the origin of the vagus nerve, all respiratory movements at once cease. Hence the medulla oblongata is, as it were, the most mortal part of the body; lesion of it is, at least, followed by more dangerous consequences than that of any other part of the nervous system.

Lesion of the nervus vagus in the neck paralyses the branches arising below the injury, therefore the nervus recurrens. The consequences are loss of voice, and difficulty in dilating the rima glottidis. The voice returns, however, in a few days, because the muscles of the larynx are supplied in common by the superior and inferior laryngeal nerves. If the superior and inferior laryngeal nerves of both sides are divided, the larynx is quite paralysed. Magendie's assertion, that the nervus laryngeus inferior supplies only those muscles which dilate the glottis, and the nervus laryngeus superior those which contract it, is not confirmed by the investigations of Schlemm and others; — both nerves are distributed to both sets of muscles. If there is any difference in the functions of the two nerves, it can arise merely from the recurrent nerve being in its remarkable course connected with the sympathetic nerve and cardiac plexus, and thus having, in addition to the voluntary motor fibres of the vagus, also fibres from the sympathetic system. It is not known whether the recurrent nerve gives the power of voluntary contraction to the muscles of the larynx. Other deep branches of the vagus which have many connections with the sympathetic nerve, such as the œsophageal and gastric branches, are no longer capable of exciting voluntary motion.

Sir C. Bell's views regarding the respiratory nerves may very properly be explained here.—The aspect of a man in a state of excited action is sufficient to prove that the movements connected with the function of respiration extend over almost the whole body; they are observable in the abdomen, chest, neck, and face. The respiratory nerves belong to

a two-fold system. One set belongs to the system of spinal nerves, with two roots,—a sensitive posterior root provided with a ganglion, and a motor or anterior which has no ganglion,—which comprehends all the spinal nerves and the nervus trigeminus. To this system belong those respiratory nerves arising from the spinal cord which serve for the motion of the thoracic and abdominal muscles. The second system of nerves which furnishes respiratory nerves, consists of those which arise by but one kind of root; the respiratory nerves of this system are the facial and vagus nerves, and the nervus accessorius Willisii. Bell supposes that a special set of fibres in the medulla oblongata and spinal cord is the source of the influence which gives rise to the simultaneous and harmonious action of the respiratory nerves of both kinds. All the respiratory nerves serve also as the principal nervous agents in the expression of the passions. A great portion of the spinal nerves concur to produce the movements of respiration; but Bell distinguishes the following as the special respiratory nerves for particular regions:

1st. The nervus vagus,—the respiratory nerve of the larynx.

2nd. Nervus facialis,—respiratory nerve of the face. The action of this nerve in respiration is more evident in proportion as the respiration is more laboured; for instance, during great muscular exertion, and in feeble debilitated persons. The elevation and depression of the alæ of the nose, and the straining of the muscles of the face, in this laboured respiration, are dependent on the influence of the facial nerve. If this nerve is divided, the sympathy of the countenance with the respiratory organs, and the expression of the passions, are lost. In brutes, the developement of the facial nerve is proportionate to the degree in which the passions are expressed by movements of their face.

3rd. The superior respiratory nerve of the trunk,—nervus accessorius Willisii, distinguished by its remarkable course. It arises by a simple root between the double roots of the spinal nerves at the upper part of the spinal cord; ascends, receiving other fibres from the medulla oblongata, into the cavity of the cranium; and issues from it again as a single nervous cord. It gives a portion of its fibres to the vagus, and directs the action of the trapezius when it co-operates in the respiratory movements, by elevating the shoulder so as to free the thorax from its weight. If the nervus accessorius is divided in a living animal, the action of the trapezius in respiration ceases; but it still retains its power of voluntary motion by virtue of the branches of spinal nerves distributed to it.

4th. The great internal respiratory nerve,—nervus phrenicus, diaphragmatic nerve.

To the posterior thoracic nerve Bell attaches too much importance.

The source whence all the nerves above enumerated derive their nervous influence is, as we have seen, the medulla oblongata. Lesion

of that part of the nervous centre puts a stop to the respiratory movements, while, according to Bell, if the spinal marrow is divided at the fifth cervical vertebra, the phrenic nerve not being implicated in the injury, respiration is still carried on by the agency of the phrenic, accessory, and external respiratory nerves; expiration being performed by the mere elasticity of the thoracic and abdominal parietes; and a new-born child, according to Bell, continues to breathe when nearly the whole brain is destroyed, if the medulla oblongata is uninjured.*

Sympathetic affections of the respiratory muscles.—I have already mentioned that the whole system of nerves engaged in the respiratory movements serve likewise for the expression of the passions. They are also affected partially, or all simultaneously, in many other cases. Nervous affections which take the form of asthma, afford an example of convulsive action of the whole system of respiratory nerves. But a fact not noticed by Bell, which nevertheless appears to me to throw much light on many phenomena, is, that local irritation of any part provided with mucous membrane is adequate to excite the respiratory system of nerves to morbid action, so as to produce convulsive motions. Irritation of the mucous membrane of the nose produces sneezing; irritation in the pharynx, œsophagus, stomach, and intestines, excite the concurrence of the respiratory movements to produce vomiting; violent irritation in the rectum, bladder, and uterus, give rise to a concurrent action of the respiratory muscles so as to effect the involuntary expulsion of the fæces, urine, or fœtus. Irritation of the mucous membrane of the larynx, trachea, and lungs, even itching from irritation in the Eustachian tube, excite coughing.

All these acts,—coughing, vomiting, spasmodic involuntary expulsion of the fæces, and involuntary discharge of urine, are effected with the aid of the respiratory movements. The first action of the local irritation affecting the inner coats of the viscera is upon the branches of the sympathetic nerve distributed to them; and in the stomach, œsophagus, pharynx, larynx, and lungs, upon the branches of the nervus vagus also; in the nostrils upon the branches of the nervus trigeminus. From these nerves the irritation is transmitted to the medulla oblongata and the spinal cord, from which is derived the nervous influence for the groups of respiratory muscles which perform the acts of vomiting, coughing, sneezing, &c. Irritation of the nasal branches of the fifth nerve produces sneezing, even when the irritation affects them indirectly, for instance, when the stimulus of the sun's light acts first on the optic nerve, and through the medium of it on the brain; from which a secondary excitement is communicated to the nasal, and at the same time to

* Sir C. Bell on the Nervous System.—Phys. Pathol. Untersuch. des Nervensystems, übersetzt von M. H. Romberg, Berlin, 1832, pp. 126—338. See also Müller's Archiv. 1834, 168.

the respiratory nerves. Like many other persons, I sneeze whenever the bright light of the sun falls on my eyes. Irritation of the vagus solely in the larynx, trachea, or lungs, excites coughing; irritation of the pharyngeal branch of the nervus vagus, and of the glosso-pharyngeal nerve, in the pharynx, or of the vagus in the stomach, excites vomiting. We will now consider, separately, each of these groups of respiratory movements.

Each individual respiratory movement can be performed singly,—sometimes, however, several are combined,—giving rise to complicated movements which are not observed in ordinary respiration.

Contraction of the diaphragm takes place at the same time with the movements of expiration, either voluntarily or involuntarily, in the act of forcible expulsion of a body from some part of the abdominal cavity: voluntarily in *the discharge of fæces and urine;* involuntarily in *vomiting, labour,* and in the *involuntary discharge of fæces or urine* after they have been too long retained. As well the pharynx as the stomach, rectum, bladder, and uterus have such a connection with the cerebral and spinal nerves, that irritation of the pharynx, or any of the other parts mentioned, excites contraction, not merely of them, but also of the abdominal muscles and diaphragm, of which the tendency is to expel the irritating body either upwards or downwards. This results from the reflection of the irritation from the branches of the nervus vagus, in the pharynx and stomach, on the brain, and from the sympathetic nerves of the stomach upon the sympathetic system, and upon the brain and spinal marrow; and in the instances of the rectum, uterus, and bladder, by communication of the irritation of the nerves of those parts, which are partly sympathetic nerves and partly branches of the sacral nerves, to the spinal cord. In all these movements, of which the object is the expulsion of a body upwards or downwards, the glottis is closed for a time.

I have observed a circumstance which is very instructive with reference to the mode of production of vomiting. If the abdomen of a rabbit is opened, and the nervus splanchnicus on the left side (on the inner side of the suprarenal capsule) laid bare and irritated with a needle, a contraction of the abdominal muscles often takes place. In the dog I have not found the same to be the case.

The act of *coughing* arises from the irritation of the nervus vagus in the larynx, trachea, and lungs being communicated to the medulla oblongata. The medulla oblongata then excites to action the muscles which produce contraction of the glottis, and at the same time gives rise to spasmodic actions of the expiratory muscles of the thorax and abdomen, during which the glottis is each time partly opened, and a loud noise produced. The diaphragm has nothing to do with the act of coughing, except that sometimes, before coughing, a deeper inspiration is taken.

Krimer* and Brachet state that after the nervus vagus has been divided on both sides, coughing cannot be again excited in an animal by irritation, however violent, of the inner surface of the trachea. While division of the sympathetic nerve is said by Krimer not to have the same effect.

We have the power of cutting off the entrance into the larynx from the nose and mouth, not merely by closing the glottis, but also, as was discovered by Dzondi, by a muscular action in the fauces themselves. It consists in bringing the posterior arches of the palate in contact from opposite sides, and in pressing the posterior part of the tongue against the inclined plane thus formed. This movement always precedes *sneezing*, which is a sudden and violent contraction of the muscles of expiration, the air passages having been previously closed at the fauces. At the moment of the violent expiration, the passage by the mouth and the nasal canal are suddenly opened simultaneously, or the nasal canal alone. The diaphragm, which so many ancient and modern authors, misled by a popular error, believed to contribute to the act of sneezing, has in reality nothing to do with it. The diaphragm is not an expiratory muscle, it only acts in producing the deep inspiration which precedes the sneezing. Extensive sympathies, which appear to be quite unnecessary, have been imagined to explain the act of sneezing, from the false notion that it is produced by the diaphragm; the irritation of the nasal nerves was supposed to be communicated to the deep branch of the vidian, and to the sympathetic; and thence to the cervical nerves and nervus phrenicus. Even Arnold still speaks of such a chain of sympathy. Since the expiratory muscles, and not the diaphragm, effect the act of sneezing, the fauces and posterior nares being first closed, the most simple view to be taken of the matter is, to consider the medulla oblongata itself as the medium of communication between the nasal branches of the fifth nerve and the expiratory muscles and the muscles of the soft palate, as the brain is in the analogous case of the sympathetic motions of the iris under the stimulus of light.†

The sympathies of a great part of the nervous system with local irritations through the medium of the brain and spinal marrow is very well illustrated by the symptoms observed in an animal under the influence of a narcotic poison, when a slight touch of the skin produces general tetanic spasms.

Yawning consists of a deep and slow inspiration and expiration, with simultaneous action of the respiratory muscles of the face. The mouth is at the same time opened wide; a movement which, like those of the facial muscles, is also under the influence of the facial nerve, being effected by means of the digastricus. Yawning occurs generally after

* Untersuchungen über den Husten.

† See the account of the nerves of the eye in the fourth book, third section, second chapter.

fatigue, and is especially frequent and easily excited in persons of irritable and debilitated nervous system; also during the state of drowsiness, and at the commencement of fever. The supposition that it arises from some obstruction in the pulmonary circulation appears to me to be quite incorrect. *Laughing* and *crying* are also attended with affections of the respiratory nerves of the face and trunk.

Hiccough is really an affection of the diaphragm,—an abrupt inspiration performed by the diaphragm alone, which sometimes contracts while the glottis is closed. It arises most frequently from some pressure on the pharynx or œsophagus, in consequence of swallowing too large morsels, or of swallowing too quickly in succession. It is frequently a symptom of affections of the nervous system. Krimer asserts that hiccough can be induced in brutes by irritating and compressing the cardiac orifice of the stomach.

All the respiratory movements are performed involuntarily, and are nevertheless to a certain extent subject to the will; they are carried on in a constant and regular succession during sleep, and at other times, without our being conscious of it; they frequently consist merely of periodic inspirations, in the intervals of which the parts return to their former state by virtue of their elasticity; frequently also there are alternate muscular actions of inspiration and expiration. If the structure of the lungs is in part destroyed or loaded with blood, a much less quantity of blood can be aerated in a given time, and the respiratory movements are then proportionally quicker. The movements of respiration are so far subject to the will, that we can, though only in a certain degree, regulate the commencement of each inspiration,—can shorten, prolong, or delay it,—and can limit the respiratory movements to single groups of the respiratory muscles; thus, for example, we can inspire with the diaphragm only, or with the ribs only, or with both at the same time. This voluntary influence is exerted in the same manner as in the case of almost all motions which are dependent on the function of the cerebral and spinal nerves; and the power of exerting it is preserved as long as the corresponding nerves are still in connection with the brain and spinal cord.

But the *regular succession of the involuntary respiratory movements* is very remarkable and difficult of explanation. The cause of the rhythm has its seat, as we have seen, like that of the movements themselves, in the medulla oblongata. In the fœtus the respiratory movements are not performed. It might, therefore, very naturally be supposed that the cause which gives rise to them is the influence of the air on the nerves distributed to the lungs, bronchi, and larynx, the irritation of the minute branches of the nervi vagi in the respiratory organs being propagated to the brain and to the source of the nervous influence which excites the respiratory movements. This explanation, however,

certainly cannot be adopted, for, if it were correct, division of the nervi vagi in the neck, and of the superior laryngeal branch, would necessarily put a stop to respiration, since the lungs and larynx would cease to be sensible to the irritation of the air: but I have done this in rabbits,—I have divided the nervus vagus on both sides, and then, having made an opening into the trachea through which respiration might be carried on, have divided also the superior laryngeal nerve, and afterwards even removed the whole larynx,—and the respiratory movements continued in the same regular succession as they do after simple division of the nervi vagi. It appears, however, from Scheele's researches, that in the fœtus the liquor amnios enters the trachea and larynx, which must therefore be in an insensible state at that period, for in the adult the smallest quantity of fluid about the glottis produces violent spasmodic action.

The cause of the first respiration appears to me to be solely the stimulus afforded to the brain, and more especially to the medulla oblongata, by the blood, which immediately becomes oxydised in the lungs. Hitherto the brain and medulla oblongata had been in a comparatively sluggish torpid condition; but the blood, as soon as the child is born, becomes arterialised in the lungs, and in a few moments reaches the brain, when the respiratory movements immediately commence.* When frogs are made to respire in hydrogen or nitrogen, the movements of respiration, after a few hours, gradually cease, because the stimulus necessary to maintain them, namely the arterialised blood, is no longer formed. If the frogs are, at this period, restored to atmospheric air, signs of life, together with the movements of respiration, return, provided the heart's contractions, although performed at great intervals, have not entirely ceased.† Bartels ‡ maintained, that the accumulation of venous blood in the brain during expiration had an effect in exciting the brain to carry on the respiratory movements. But Treviranus § tied the blood-vessels in frogs, and the respiratory movements still continued; and Legallois || saw the mouth of rabbits open and shut repeatedly, as if to respire, after the head had been separated from the body.

Effects of division of the vagus nerves.—Division of the recurrent nerve on both sides is, as Legallois observed, often mortal in young animals; in the adult it is not so. Division of one nervus vagus does not cause

* [The above theory does anything but satisfactorily explain the commencement of respiration. It is probable, certainly, that the brain, on receiving a supply of arterial blood, becomes better enabled to perform all its functions; but, before arterialised blood can reach the brain, respiration must have commenced. The question is then, how does the blood first become arterialised,—how is the air first drawn into the lungs? This question is not answered by the hypothesis in the text.]

† See the experiments of Professor Bergemann and myself, at pages 339 and 340.

‡ Die Respiration als vom Gehirne abhängige Bewegung und als chemischer Process. Breslau, 1813, 99. § Biologie, v. p. 260. || Loc. cit. p. 29.

death; but the simultaneous division of both nerves is always fatal, death taking place in a few days. The causes of death after this operation have occupied the attention of physiologists since the time of Rufus Ephesius and Galen; more recently the inquiry has been instituted in a better manner, but the proximate cause of death is still unknown. The movements of respiration are, for the most part, unaffected by the injury. The recurrent nerves, and consequently the muscles of the larynx, are half paralysed by it; but division of the recurrent nerves alone is not attended with a fatal result. Dupuytren found that when the two nervi vagi were divided in a horse, death, preceded by gradually increasing difficulty of respiration, ensued within an hour; in a dog within two or three days. The blood in the carotid arteries became gradually of a venous colour. Hence it was inferred that the chemical process in the lungs was interrupted by the division of the nerves, an inference which was rendered improbable by the mere circumstance that blood, even out of the body, undergoes the same changes as take place during respiration.*

Soon afterwards, indeed, Blainville† showed, by experiments, that birds consume as much oxygen, and exhale as much carbon, after the nervi vagi have been divided, as in the natural state, and that the colour of the blood undergoes the same change in the lungs. Birds live a considerable time,—six or seven days,—after this operation. Rabbits die in about thirty hours. In birds there is complete wasting of the body before death. Hence Blainville attributes the death to the disturbance of the digestive function; an explanation, however, which, at all events, is not applicable to rabbits and mammalia generally. Dumas‡ found that inflation of the lungs with atmospheric air or oxygen restores the scarlet colour to the arterial blood. In Emmert's§ experiments on rabbits, the respiration became less frequent, slower, and more laboured after the nervi vagi were divided. This is a constant result, and is, in fact, very interesting; I have myself observed, both in rabbits and birds, that, from the moment in which both nerves were divided, the inspirations became deep and slower. Emmert did not find that the changes which the blood undergoes in the lungs were much affected; he attributes the death of the animals in part to paralysis of the peculiar motion of the bronchi. At the same time he has pointed out, that, in the rabbit, the sympathetic nerve and nervus vagus remain separate in the neck, while they become united just below the superior cervical ganglion in most mammalia, in which consequently the nervus vagus cannot be divided or tied without the sympathetic nerve being also implicated. (Bischoff||

* For a critique on these observations I refer to the excellent treatise of Emmert, mentioned below, which contains the most complete account of the earlier experiments connected with this subject.

† Nouv. Bullet. de la Soc. Philos. 1808.

‡ Journ. Gén. d. Médec. t. xxxiii. 1808, Dec.

§ Reil's Archiv. ix. 380; xi. 117.

|| Nervi accessorii Anatomia et Physiologia. Heidelb. 1832.

states that the hog, (?) rabbit, mole, and wood-mouse are the only mammalia in which the vagus and sympathetic nerves are not firmly connected; according to my observation the connection does not exist in the porcupine likewise.) Emmert therefore attributed the different result of the experiments of Dupuytren, Blainville, and others, to the circumstance of one or both of the nerves having, in different cases, been divided, according to the animal employed. In Dupuytren's experiments on the horse both nerves were divided; in Emmert's experiments on rabbits, and in Blainville's on rabbits and birds, the nervus vagus only was divided. V. Pommer's experiments, however, prove that this difference can have no particular influence on the result; for he found that division of the sympathetic nerve, on both sides of the neck in brutes, was attended with no important consequences whatever. His experiments were made on rabbits and dogs; in the latter animal the sheath that contains the nervus vagus and sympathetic was laid open, and the sympathetic alone divided. At the end of seven or eight weeks,—as long as they were observed,—the animals showed no particular signs of inconvenience.* Arnemann asserts that division of both nervi vagi is not always fatal to dogs.

In Provençal's experiments† the chemical changes of respiration seemed still to go on, but in a diminished degree, when both nervi vagi were divided. The animals consumed less oxygen, and formed less carbonic acid, and their animal heat was lowered. Legallois, who had previously observed that, under ordinary circumstances, an animal lives longer without respiring the younger it is, found the contrary to be the case after division of the nervi vagi. A new-born puppy dies in half an hour after that operation has been performed, while a full-grown dog lives one or two days; in young animals, also, division of the nervi recurrentes is fatal in half an hour; so that, in young animals, the cause of the rapid death after division of the nervi vagi seems to be the simultaneous paralysis of the inferior or recurrent laryngeal nerves, and of the muscles of the larynx. Hence tracheotomy prolongs life somewhat in young animals under these circumstances. Legallois also ascertained that the glottis, which is naturally dilated during inspiration, is almost wholly closed in young animals after this operation. One consequence of division of the nervi vagi observed by Legallois was the effusion of a bloody serous frothy fluid into the lungs, which must increase the dyspnœa produced by the paralysis of the muscles which dilate the glottis. These two causes united, when the nervi vagi are divided, seem to produce the final suffocation and death which follow division of the nervi vagi, and which do not occur in adult animals when the recurrent nerves merely are divided. Horses and sheep, in which Dupuy divided both vagi, died within an hour unless tracheotomy was performed, when they lived several days. In these experiments of Dupuy the effect of paralysis of the

* Refer to page 198.

† Journ. Gén. de Méd. 37. 1810, Janv.

recurrent nerves is separated, as it were, from the effect of paralysis of the pulmonary branches of the vagus. Dupuy believes, however, that the paralysis of the lungs produces suffocation not merely by the effusion of fluid, but also by the diminished respiration. The cause of the effusion of fluid from the pulmonary vessels into the air cells and bronchi is easily understood from the considerations offered on exudation at page 255.

The assertion of Krimer, that an effusion of fibrin takes place into the air cells after division of the nervi vagi, if correct, is important.

Mayer* observed as a constant result of the numerous experiments in which he tied or divided the nervus vagus, that, when death takes place long—forty-eight hours or more—after the operation, firm white coagula are found in the blood of the lungs and heart, and completely fill the cavity of the vessels, as well as of the heart. The coagula were soft and black when death followed the operation quickly. These observations are very interesting. But I have repeated the experiments without obtaining the same result. A second phenomenon and cause of death, which, according to Mayer, occurred frequently after division of the vagi, though certainly not in all cases, is the regurgitation of the food from the stomach, and its entrance through the relaxed and insensible glottis into the trachea and bronchi. Mayer observed, too, that after the operation of which we are speaking, the heart's action becomes much accelerated, the respiration gradually slower.

A consideration of all the different results obtained by the various observers leads to the inference that death, after tying or dividing the nervus vagus, arises from the concurrence of different circumstances, which at last produce suffocation. They are the following:—1. Incomplete paralysis of the muscles of the glottis. 2. Exudations in the lungs. 3. Change in the chemical process going on in the lungs. 4. Coagulation of the blood in the vessels, as observed by Mayer.†

SECTION II.

Of nutrition, growth, and reproduction.

CHAPTER I.

OF NUTRITION.

a. Of the nutritive process.

The process of nutrition is not an object of microscopic observation.‡ The theory, that nutrition is effected by the direct union of the red particles of the blood, or of their nuclei, with the tissues, is, in my opinion, decidedly erroneous. The perfection at which micrometry has arrived, and the use of good instruments, have made us now so well acquainted

* Tiedemann's Zeitschrift für Physiol. ii. 74.

† On this subject refer to Lund, Vivisectionen, pp. 222—243. ‡ See pages 221, 222.

with the physical properties of the organic tissues, that we are enabled to refute the above theory, by merely comparing with precision the size of different parts.

Microscopic admeasurements, if intended to serve as the basis for scientific researches and comparisons, must not consist merely in the direct measurement of each object; a much more important and essential mode of investigation is the comparison of the object to be measured with some other body that can be taken as a standard. Thus, for instance, in measuring the size of the muscular or nervous fibrils, they should be placed under the microscope, together with red particles of human blood, and both should then be observed at the same time. The admeasurements of the red particles of human blood, as stated by Kater, Wollaston, Prevost and Dumas, Weber, Wagner, and myself, agree so nearly,* that their diameter may with great certainty be stated at $\frac{1}{4600}$ of an inch English. We have thus a certain standard of measurement. As standards of comparison, I employ the red particles of human blood, easily obtained by slightly scratching the skin,—those of frog's blood, which are about four times larger in diameter,—and the nuclei of these latter bodies, obtained by the action of acetic acid, which measure about $\frac{1}{4}$th or $\frac{1}{3}$rd the long diameter of the entire red particle.

It has been said that the red particles of the blood agree in form with the elementary particles of which the tissues of the body are composed, which is evidently not correct; besides the red particles of the blood in all vertebrata have a compound structure,—they are composed of two parts, the nucleus, and an outer envelope. The muscular and nervous fibres have been said to be formed of aggregated globules; but the red particles of the blood are not globular in any vertebrate animal, they are flattened in the form of disks. Prevost and Dumas, and Edwards, regard the nuclei of the red particles as the elements of which fibres are formed; but my observations do not confirm their views. I have never been able to satisfy myself that the primitive fibrils of muscles and nerves consist of aggregated globules. The muscular fibrils appear to me to be merely fibres with enlargements succeeding each other very closely. C. A. Schultze† has also failed in perceiving the globules of muscular fibre. Still less do the nervous fibrils appear to me to have the structure alluded to; they are for the most part uniform fibres, with merely inequalities of the surface. In the glare of the direct light of the sun they appear (like all other tissues by this light,) to consist of globules, but these globules cannot be distinguished from inequalities of the surface, which put on the appearance of globules. I am not speaking of the varicose enlargements of the fibres of the brain and spinal marrow, which Ehrenberg has discovered; *these* are separated by considerable and uniform interspaces.

* See page 101.

† Vergleich. Anat. 123.

The red globules of frog's blood have, according to my observations, a diameter from five to eight times greater than that of the primitive fibrils of their muscles. The diameter of the red particles of rabbit's blood is from five to six times greater than that of the primitive muscular fibre of the same animal, which, after they have been rendered visible by maceration for fourteen days (in winter), are seen to be knotted, and to resemble a string of pearls. The primitive fibres of nerves, which are thicker than muscular fibrillæ, also do not correspond in size with the red particles of the blood and the nuclei of these bodies. The nuclei of the red particles, besides, are not globular in the amphibia, but elliptic, and in the salamander they are even flattened; how, then, can the primitive fibres of nerves and muscles be formed of them?

The most minute capillary vessels are not distributed to the primitive fibrils of nerves and muscles; these fibrils are too fine to receive vessels, and are, in fact, more minute than the capillary vessels themselves, which measure from $\frac{1}{4600}$ to $\frac{1}{1850}$ of an English inch in diameter. Nutrition, therefore, must be effected through the coats of the capillary vessels, and the process consists in the fluid parts of the blood permeating the parietes of the capillaries, while the solid particles are visibly carried onwards into the veins. The most important materials for nutrition are the albumen and fibrin dissolved in the liquor sanguinis. A portion of these matters permeate the parietes of the capillaries, and are imbibed by the tissues; and what is effused over and above the quantity required for their nutrition, is taken up by the absorbent vessels, and carried again into the blood. It is here of importance to know that the capillaries really have solid parietes; the proofs of which were stated at page 216. Nothing can pass from the blood to the tissues, or from the tissue to the blood, without permeating, in the fluid state, the walls of these vessels. The hypothesis of the blood flowing in simple canals excavated in the substance of the organs, appears at first sight calculated more easily to explain the problem of nutrition, but is found on examination to be untenable. The permeable parietes of the capillaries are, in fact, no impediment to the process of nutrition, which appears to consist in matters dissolved in the blood being attracted from it by the organic particles contained in the meshes of the capillaries, while at the same time the old materials of the particles are returned into it. Wildbrand certainly did not employ the microscope when he formed his hypothesis of the metamorphosis of the blood in the small vessels.

It is not known whether the parts which appear to contain colouring matter, as, for instance, the muscles, derive it from the blood,—a part of the colouring envelope of the red particles having been dissolved,—or whether this matter, which becomes still more highly coloured by the action of the atmosphere, is formed in the muscles themselves. But, however this may be, the red particles themselves do not unite in sub-

stance with the tissues. They certainly perform some very important office in the animal economy. In their passage through the lungs they acquire the bright arterial colour, and in their subsequent transit through the capillaries of the body a reciprocal action takes place between them and the component particles of the organs, by which they lose this bright colour, becoming again of a dark red; but they still move on in a continuous current, exerting their influence on the tissues in their transit through them, without being arrested by them. In each circuit of the blood, which occupies less than three minutes,* they undergo two changes of colour; one from dark red to bright scarlet in the lungs, and another from scarlet to dark red in the capillaries of the body. In twenty-four hours each of these changes takes place about 480 times. In their arterialised condition the red particles exert on the organs of the body, and especially on the nerves, a stimulating action, which is essential to life, but which is a very different thing from contributing new nutritive matter. Dutrochet believed that the red particles have peculiar electric properties, an opinion which has been already refuted in Chapter III. of the section on the Blood.

In the process of nutrition is exemplified the fundamental principle of organic assimilation. Each elementary particle of an organ attracts similar particles from the blood, and, by the changes it produces in them, causes them to participate in the vital principle of the organ itself. Nerves form nervous substance, muscles muscular substance, even morbid structures have the assimilating power;—warts on the skin grow with their own peculiar structure; in an ulcer the base and border are nourished in a way conformable to the mode of action and secretion determined by the disease; and the assimilation of the nutrient materials of the blood to form an organ with diseased action may induce the destruction of the life of the animal.

The proximate elements of the tissues exist in part ready formed in the blood. The albumen which enters into the composition of the brain and glands, and of many other structures in a more or less modified state, is contained in the blood; the fibrin of the muscles and muscular structures is the coagulable matter dissolved in the lymph and blood; the fatty matter which contains no azote, exists in the free state in the chyle; the azotised and phosphoretted fatty matter of the brain and nerves exists in the blood combined with the fibrin, albumen, and cruorin. The iron of the hair, pigmentum nigrum, and crystalline lens, is also contained in the blood; the silica and manganese of the hair, and the fluor calcium of the bones and of the teeth, have not hitherto been detected in the blood, probably from their existing in it in but small proportion. The matters here enumerated are attracted from the blood by particles of the organs analogous to themselves, partly in the state in which they afterwards exist in the organs; in other instances their

* See page 186.

ultimate elements are newly combined in them, so as to form new proximate principles; for the opinion that all the component elements of the organs exist previously in the blood in their perfect state, cannot possibly be adopted: the components of most tissues in fact present, besides many modifications of fibrin, albumen, fat, and osmazome, other perfectly peculiar matters, such as the gelatine of the bones, tendons, and cartilages,—nothing analogous to which is contained in the blood. The substance of the vascular tissue, the different glandular substances also, cannot be referred to any of the simple components of the blood. Even the fibrin of muscle cannot be considered as exactly identical with the fibrin of the liquor sanguinis; for between coagulated fibrin and coagulated albumen there is scarcely any chemical difference, except in their action on peroxide of hydrogen: the only very important distinction between the fibrin dissolved in the blood and the albumen is, that the former coagulates as soon as it is withdrawn from the animal body, while the latter does not coagulate spontaneously, but requires a heat of from 158° to 167° Fahr., or some chemical agents, such as acids, concentrated solutions of fixed alkali, or metallic salts; and the fibrin of muscle in its chemical characters has scarcely a greater analogy with coagulated fibrin than with coagulated albumen. In its vital properties the fibrin of muscle differs from both. The comparison of nervous substance, again, with albumen and fatty matter containing nitrogen and phosphorus, is only justified by the present imperfect state of organic chemistry.

Assimilation, then, does not consist merely in the component particles of the organs attracting the fibrin, albumen, and other matters of the blood which flows through them, adding to themselves the matters similar to their own proximate principles, and changing the composition of those which are dissimilar; besides these actions, the assimilating particles infuse into those newly assimilated their own vital properties. Organs may increase in size, independently of assimilation; thus, in inflammation, the albumen and fibrin of the blood accumulate, unassimilated, between the particles of the tissues; and this sufficiently marks the distinction between inflammation and hypertrophy, or increased nutrition. In the pregnant state, the contractile tissue of the uterus increases in bulk by the addition of real contractile particles, duly assimilated to the original tissue, but in inflammation of the uterus nothing of this kind is observed; in inflammation the assimilating power is arrested, the fibrinous fluid exudes through the membranes, or collects in the interstices of the tissue of the organs: the matter, therefore, which increases the volume of the inflamed organ is the same, whatever the organ may be; while in the process of nutrition, the components of the blood assimilated by the different tissues are, in each case, differently modified and changed. Inflammation, then, is not an increased degree of the plastic or nutritive process. From these considerations, too, it is

easy to understand why a stimulus which promotes the action of an organ, is very different from one which excites inflammation.

There are several substances which are known to diminish the activity of the assimilating process, by effecting a change in the composition either of the organ or of the blood. Iodine, for example, when its use is long continued, has a remarkable effect in diminishing nutrition. The neutral salts, mercurial medicines, tartarised antimony, and other substances, have the same effect on the system. The immediate action of these substances is partly to produce a change in the blood, as is evident in the case of the cooling salts, which when added to the blood, even out of the body, deprive it of its property of coagulating, of course by a change produced in the fibrin; and it is on this account that these substances are of importance in checking inflammation.

The circulating fluids—the chyle and blood—sometimes acquire an anormal composition, either from the new nutrient matters from which they are formed not having themselves their natural healthy composition, or in consequence of the operation of an inoculated virus, as that of syphilis. In all these cases, in which the circulating fluids are diseased, nutrition also suffers. Depositions of morbid matter, inflammations, and sores, occur, as in scrofula, gout, lepra, herpes, scurvy, syphilis, &c. All the diseases here enumerated, although very different in themselves, have the common character of manifesting themselves by the secretion of morbid matters on the skin, by eruptions and sores of the surface, frequently ulcers of the mucous membranes, and in extreme degrees by morbid affections of the bones. Several medicines which themselves have the power of modifying the assimilating process,* and, when long used, also produce ulcers and diseases of the bones,—mercury and antimony, for instance,—are sometimes of service in some of these diseases, not on the principle that *similia similibus curantur*, but because they produce such an alteration in the composition of the tissues, that the affinities already existing are annulled and new ones induced, so as to enable the vital principle—the power which determines the constant reproduction of all parts in conformity with the original type of the individual—to effect the further restoration and cure; the mercury itself does not complete the cure. In several of the diseases in which the fluids of the body are in a morbid condition, the lymphatic system—the absorbent vessels and glands—is likewise particularly liable to suffer. Regarding this system in the ordinary way as merely intended for absorption, it is difficult to understand why it should be implicated in many of these diseases, particularly in scrofula. But when it is known that the lymph is almost identical with the liquor sanguinis, both containing fibrin and albumen in solution, and that the portion of the liquor sanguinis effused into the tissues for the purpose of nutrition, which exceeds

* See the observations on alteratives, p. 59.

the quantity necessary for this object, is removed by the lymphatics, which, moreover, have a great share in the conversion of the albumen into fibrin,* it is easy to conceive that a change in the composition of the liquor sanguinis, which causes irritation and inflammation in the capillaries, must also excite irritation in the lymphatics,—the fluid which circulates in them being one and the same. All the other substances contained in solution in the blood, besides the albumen and fibrin,—the salts, for example,—and their morbid composition, must also have great influence on the state of the lymphatics. In those diseases in which it is not so much the fluid ingredients of the blood that are morbidly changed, as the cruor or red particles, which do not enter the lymphatic vessels, as in scurvy, these vessels and their glands present less evident appearances of disease. The foregoing remarks are sufficient to show that the future study of the morbid states of the fluids of the body will find a surer basis in the analysis of the lymph and blood which we have offered, than in the older notions regarding these fluids.

The nutrition of all parts of the body in conformity with the original type presupposes the persistence of that power which produced all the distinct parts—all the organs—originally as "members of the whole,"—as parts necessary to our idea of the being,—and which exists in the germ before any distinct organs are formed, when the animal exists as yet merely "potentially" in the form of the germ.† Nutrition, then, is the continued reproduction as it were of all the parts of the animal by this internal power: but in the adult the reproduction can only be effected by the process of assimilation, that is, by the union of new matter with the assimilating parts; while in the embryo, in which no organised "groundwork" as yet exists, the parts are formed—their "groundwork" in fact created—by the formative power which is still undivided. However, until the whole body is destroyed, all the organs are directed by *one* formative principle so as to produce the concurrent action of all assimilating tissues; it is the operation of this principle that we admire, as the *vis medicatrix naturæ*, in the correction of the subtle material changes which are induced by diseases; but organized parts of the body once formed cannot in most cases, if wholly destroyed, be again restored by this power.

In some diseases there is such a morbid formation of the animal matter, that the assimilation of the fluids to form the natural elementary tissues of organs is in certain parts of the body wholly arrested, and, on account of the predominance of anormal affinities, non-analogous tissues, such as cancer and medullary fungus, are formed.

Life is attended with a constant change of the material of the body. This is evidenced by new nutriment being required in proportion to the quantity of the excretions. The question, however, presents itself—Do

* See page 283. † See page 23.

the components of the fluids merely undergo this change, or are the particles of the organised tissues also renewed?

1. *Renewal of the material of the fluids.*—It is most natural to suppose that the change of material takes place primarily in the fluids of the body, and that the fluids only are implicated in the change by which several pounds of nutriment are received daily in place of several pounds of decomposed matters, which are expelled in the cutaneous transpiration, in respiration, with the urine, and other excretions, and that the solids themselves have little share in it. The fluids, while they maintain the life of the body, are constantly undergoing decomposition, and in this respect the animal machine might be compared with other machines,—for example, with the steam-engine, which requires a certain quantity of fuel for the generation of the steam, on which its action depends. There is no doubt but that the change of material is greatest in the fluids; it is indeed sufficiently proved by the fact that the excretion of urine takes place at very long intervals in reptiles—tortoises, for instance—which are kept without food. It may be supposed that the decomposition which a certain quantity of the fluids suffers in the performance of their function of supporting life, renders necessary the excretion of the decomposed matters, and the supply of new nutriment.

2. *Renewal of the material of the organised solids.*—There are many phenomena which it appears difficult to reconcile with the idea of the renewal of the animal matter in the organised solids; for example, the preservation of past ideas, which are the result of certain impressions made upon the sensorium. Whatever share these impressions on the sensorium, and the unknown subtle material modifications produced by them, may have on the operations of the mind in the exertion of the faculty of memory, it cannot be questioned but such material changes of the sensorium do take place; for organic change of the sensorium produces change or diminution in number of the impressions previously accumulated, and annuls the faculty of recalling single chains of ideas; for example, the memory of the structure of languages, and, it appears, even of particular parts of speech,—substantives, proper names, &c.—the remembrance of certain places, and of certain periods of past life. How now can the existence of memory,—the intellectual life of man,—as a state resulting from the past developement, be imagined, if a great change in the materials composing the brain and nerves is admitted to take place? The change of material appears to be very slight at all events in the brain and nerves. If it be admitted that it does take place, it must be supposed that the particles of the brain on which depend the preservation and retention of certain ideas, transfer their peculiar state to the new matter which replaces them, just as in a wart on the skin the peculiar composition and form of the particles is preserved during the process of assimilation, and as, during the constant destruc-

tion which a fungus suffers, the reproduction of its tissue takes place with the same form and composition.

In most parts, the nerves excepted, there are many unequivocal signs of the change of material; and the bones themselves, which at first sight appear the most fixed and stable parts of the body, and nevertheless exhibit such distinct traces of renewal of their material, seem to prove that this process is not limited to the fluids of the body, but is a phenomenon which prevails extensively even in the organised solids. Among the evidences of the renewal of the material of bones are the formation of the cells, the developement of the frontal and sphenoidal sinuses in childhood, the absorption of bones under the pressure of swellings, the absorption of the alveoli of the jaws, and the thinning of the cranial bones in old age, &c. The enlargement of the cavities of the bone, with enlargement of the whole bone itself, and indeed the mere growth of so solid a body by interstitial assimilation, and the changes that its form undergoes during growth, are not conceivable without a constant removal of osseous particles from certain parts, and the deposition of similar particles at other parts, consequently not without a change of material. In other parts of the body the proofs of the renewal of the substance are less evident. Such proofs, however, are found in the constant decomposition on the surface of a fungus, as of fungus hæmatodes, concurrently with its reproduction,—in the wasting of the solids of the body during abstinence from food, in atrophy, and in several chronic diseases,—and in the growth, change of form, and wasting of tumours and warts, and their frequently rapid reproduction after previous wasting. The parts removed in these cases must be received either into the blood-vessels or into the lymphatics, when these latter vessels exist in the part. It would be incorrect, however, to regard the lymphatic absorption as the mere resumption of the previously organised particles of the solids into the fluids, and the lymph consequently as a mere solution of the solids; for, with the exception of its globules, the lymph consists, as we have seen,* of liquor sanguinis, and is derived from that part of this fluid which is effused into the tissue of the organ, and is not required for nutrition.

The exchange of old for new matter in the solids of the body might be presumed, if merely from the constant changes which are taking place in the form of parts. From childhood upwards the organs are continually changing their form, and this change in the form of the whole organ can only be effected by means of a change in the minute elementary particles which compose it. In this change it may be imagined that the particles absorbed are taken up into the blood, and are soon employed again for the purpose of nutrition at other points. But it still remains for us to inquire whether there does not exist a process of renewal of the constituent matter of organs in which the old and de-

* See pages 145 and 258.

composed materials are taken up into the blood for the purpose of being expelled from the body. Unfortunately, the only facts that we are in possession of by which this question can be determined, are, the termination of life generally, and the certainty that in old age the accumulation of useless elements in the tissues is constantly increasing, that the quantity of animal matter in the bones diminishes,* and that calcareous matter is deposited in the coats of arteries and other parts. D'Outrepont† supposes that life itself subsists with, and consists merely in, a constant exchange of material in the fluids and organized solids. It has already been shown that life is attended with a constant decomposition of the material of the body. Every action produces a change in the composition of the active part, and excites a call for the restoration of the natural composition, which is gradually effected during the state of rest. It appears therefore really that even the organized solids undergo a gradual decomposition of their component particles, which is inseparable from their state of action, and which itself induces renovation.

In the Prolegomena on General Physiology‡ I have stated all that is known respecting the balance between the destruction of material produced by the state of action and the renovation which succeeds; but, unfortunately, all such delicate relations cannot be subjected to calculation. We have here only very imperfect data, such as the fatigue after action, and the necessity for a large quantity of stronger nourishment after great mental or muscular exertion; while, on the other hand, the permanence of certain colouring matters introduced into the skin point out a limit to the process of absorption and renovation. Within these limits, too, the indications of the renewal of the substance of the organised solids are of very various degrees of distinctness: we may instance, for example, the frequently quick disappearance of warts from the skin; the rapid absorption of bones, and their rapid union after fracture; lastly, the very gradual reduction of a shapeless callus to a form corresponding more nearly to the natural outline of the bone, during which process the cavity of the bone is restored at the point of fracture, sometimes after the expiration of months; while, on the contrary, the difficulty with which specks of the cornea are removed, shows us how the renovating process here stands in an inverse ratio with the paucity of blood-vessels.

The exchange of material, lastly, is most considerable in youth, and diminishes more and more as age advances.

b. Chemical composition of the organised tissues.§

1. *The brain, spinal marrow, and nerves.*—The fatty matter of the

* See page 370.

† Diss. de perpetuâ materiei organico-animalis viciss. Hal. 1798. Reil's Archiv. iv. 460.

‡ Page 52.

§ After Berzelius, Chimie Animale. The seventh volume of his Traité de Chimie, translated by Esslinger and Jourdain.

brain is extracted by treating the cerebral substance previously rubbed to a pulp, with boiling alcohol or ether; what remains is the albumen of the brain and the fragments of vessels. The cerebral fatty matter consists of azotised elaine and stearine. The first is an oily substance, having the smell of the fresh brain and a rancid taste, and suffers putrefaction like other animal substances when exposed to the air. It is more soluble in boiling than in cold alcohol. The stearine is in the form of white scales of a satiny lustre. Gmelin and Kuehn distinguish in this substance two kinds of stearine; the one lamellated, the other in the form of a powder. The first is similar to cholesterine, but is distinguished from it by containing phosphorus. The fatty matter of the brain differs from other kinds of fat in two characters; it does not, according to Vauquelin, unite with alkalies, or form soap; and, moreover, it contains phosphorus. Chevreul and Braconnot, however, have also found phosphorus in the fatty matter which exists in a combined state in the blood and in the liver. The cinder which remains after combustion of the adipose matter of the brain contains so much phosphoric acid as to prevent the access of air which is necessary for its complete calcination. If the phosphoric acid is removed by means of water, the cinder again burns for a time, but the combustion ceases when more phosphoric acid is formed. Hence it appears that the phosphorus in the cinder of cerebral fat is not in a volatile state. Vauquelin calculated that the quantity of phosphorus in fresh brain was as much as 1 per cent. or $\frac{1}{3}$ of the weight of the fatty matter, which Berzelius considers improbable. The other components of the brain are albumen and salts—phosphates and carbonates of an alkali. The result of Vauquelin's analysis of the brain is as follows:—

Albumen		7·00
Adipose matter	Stearine 4·53, Elaine 0·70	5·23
Phosphorus		1·50
Osmazome		1·12
Acids, salts, and sulphur		5·15
Water		80·00
		100.00

The proportion of earthy and saline ingredients in the brain is extremely small. From fifty grains of dried brain of the calf, Dr. John obtained only two grains of ash; from 100 parts of dried cerebral substance, Sass and Pfaff obtained 3·36; while from 100 parts of dried muscle they obtained 7·5 parts of fixed salts.*

Dilute muriatic acid, according to Reil, dissolves the neurilema of the nerves; while alkaline solutions, on the contrary, dissolve the nervous matter.

* For an account of the investigations of different chemists on the composition of the cerebral substance, refer to E. H. Weber's edition of Hildebrandt's Anat. t. i. p. 257.

2. *Muscle.*—Muscular substance is hardened by long boiling, and yields a colourless liquor, which, on cooling, becomes a gelatinous mass; the coagulation arises from the presence of gelatin, into which the cellular tissue, according to Berzelius, is converted by boiling. Acids and alkalies have the same action on muscle as on fibrin. Muscular substance, cut in pieces and subjected to a strong pressure, yields a red acid fluid, which contains, 1. albumen and cruorin; 2. lactic acid; 3. salts—the lactates of potash, soda, lime, and magnesia, traces of lactate of ammonia, chlorides of potassium and sodium soluble in alcohol, and phosphates of soda and lime insoluble in alcohol; 4. extractive matter soluble in alcohol—osmazome, which has the smell of the flesh, and which, according to Berzelius, is a mixture of many substances,—and extractive matter soluble in water—an acid substance containing lactic acid, which is itself a compound of several substances soluble in water, among which is zomidin, which has the flavour of the meat. Muscle treated with concentrated sulphuric acid forms a substance called leucine, which has the flavour of the broth of the meat.

We have two analyses of the muscle of the ox, by Berzelius and Braconnot.

		Berzelius.	*Braconnot.*
Muscular fibre, vessels, and nerves	15·8 }	17·70	18·18
Cellular tissue by boiling converted into gelatin	1·9 }		
Soluble albumen and colouring matter		2·20	2·70
Alcoholic extract with salts		1·80	1·94
Watery extract with salts		1·05	0·15
Phosphate of lime with albumen		0·08	
Water and loss		77·17	77·03
		100·00	100·00

Sass and Pfaff* have instituted comparative analyses of muscle and cerebral substance, of which the following is the result:

	Muscle.	*Brain.*
Carbon	48·30	53·48
Hydrogen	10·64	16·89
Nitrogen	15·92	6·70
Oxygen	17·64	18·49
Fixed salts	7·50	3·36
Phosphorus		1·08
	100·00	100·00

Muscle, then, appears to contain much more nitrogen, and cerebral substance a greater proportion of hydrogen.

3. *The bones.*—By macerating bones in diluted muriatic acid the earthy matter is removed, leaving the cartilage, which by boiling is wholly converted into gelatin. The earthy matter of the bones of the higher animals consists chiefly of phosphate of lime, with carbonate of lime and a small quantity of phosphate of magnesia and fluate of lime. The phosphate of lime of the bones is a subsalt, in which the base and acid are combined in peculiar proportions, and which is always obtained when biphosphate of lime is precipitated by an excess of ammonia. The

* Meckel's Archiv. v. 332.

phosphate of lime of the urine is a supersalt, and is in solution, and in the disease called mollities ossium seems to be excreted in a state of solution in the urine in larger quantity than natural. The following is the result of Berzelius's analysis of the bones in man and the ox:

	Man.	*Ox.*
Cartilage completely soluble in water	32·17	53 30
Vessels	1·13	
Neutral phosphate of lime	51·04	55 45
Carbonate of lime	11·30	3·85
Fluate of lime	2·00	2 90
Phosphate of magnesia	1·16	2·05
Soda, with a small proportion of chloride of sodium	1·20	2·45
	100·00	100·00

Schreger states that, in the bones of a child, the earthy matter constitutes $\frac{1}{2}$, that in the bones of an adult it amounts to $\frac{4}{5}$ths, and in those of an old person to $\frac{7}{8}$ths of the whole mass.*

The existence of the phosphate of lime in the bones in the state of a salt is proved by the affinity evinced by the rubia tinctorum for the bones of living animals, which it colours red.

4. *Cartilage.*—The cartilages of the cartilaginous fishes yield, after forty-eight hours' boiling, but not till then, a glutinous substance, which is precipitated by infusion of galls, but which does not, like real gelatin, become gelatinous on cooling; in this particular my observation is opposed to that of Chevreul. In man there are some cartilages which do not afford gelatin when the coction is not continued for a very long time: such are, according to Berzelius, those which cover the articular ends of bones; the cartilages of the nose, ear, eyelids, larynx, and trachea, according to Weber and Berzelius; and, according to Weber, the costal cartilages. Berzelius obtained gelatin from the cartilages which unite bones immoveably by synchondrosis, and from the costal cartilages, which in old age become ossified. The costal cartilages of a man of twenty years yielded an ash, from which Frommherz and Gugert could not entirely get rid of the carbon by calcination; 100 parts of the ash of this cartilage contained

Carbonate of soda	35·06
Sulphate of soda	24 24
Chloride of sodium	8·23
Phosphate of soda	0·92
Sulphate of potash	1·20
Carbonate of lime	18·37
Phosphate of lime	4·05
Phosphate of magnesia	6·90
Oxide of iron and loss	0·99
	100·00

In the cartilage of a female, aged sixty-three years, the same soluble components were present in smaller proportion; and the phosphate of lime was in larger proportion than the carbonate of lime. Cartilage contains two-thirds of its weight of water.

* Hildebrandt's Anat. by Weber, t. i. 316. On the composition of diseased bone, see Bostock, in the Medico-Chir. Trans. vol. iv.

5. Of the different *glands*, the liver and kidneys have been subjected to a chemical analysis. Braconnot rubbed the substance of the liver of an ox to a pulp, and then macerated it in water, when the greater part of it was dissolved. The milky fluid thus obtained coagulated by heat; and the coagulum, when treated with oil of turpentine, yielded a fatty oil, which remained after the volatilisation of the turpentine, was of a red brown colour, was half congealed, and had the peculiar smell and taste of the liver of the ox. It was not acid, therefore not in a saponified state; but formed a soap with caustic soda, without ammonia being developed. This fat contains phosphorus, and presents the same phenomena during its combustion as the fatty matter of the brain.

The solution of the liver, from which albumen was precipitated by heat, reddened litmus-paper, and appeared to contain a substance not very unlike osmazome; 100 parts of the substance of the liver were found by Braconnot to consist of

Water	68·64
Albumen	20·19
A matter containing little nitrogen, easily soluble in water, and slightly soluble in alcohol	6·07
Fatty matter of the liver	3·89
Chloride of potassium	0·64
Lime, with iron	0·47
Salt of a combustible acid with potash	0·10
	100·00

Frommherz and Gugert state that they have also found casein and salivary matter in the human liver. From the liver of the ray, Vauquelin obtained an oil which constituted more than half its weight. Berzelius concludes, from his researches, that the liver contains an emulsion-like combination of albumen with a fatty substance, mixed with other animal matters, such as osmazome, and one or two other substances, insoluble in alcohol and soluble in water.

The *kidneys* of the horse have been analysed by Berzelius. The substance of the organ, rubbed to a pulp and triturated with water, became almost wholly a milky fluid. The small quantity of fibrous matter which remained consisted, probably, of vessels. The fluid mass coagulated on the application of heat. The coagulum consisted of albumen and a considerable quantity of fatty matter. The fluid which remained after coagulation contained free lactic acid, and some animal matter, which, after evaporation, was soluble partly in alcohol and partly in water.

The chemical properties of the *fibrous coat of arteries* have been already stated at page 203. The analysis of the *hair* and other *horny structures*, of the *teeth* and *crystalline lens*, will be found in the following chapter.

The *serous membranes* are said to yield gelatin by boiling, and in this character agree with *cellular membrane*. All that is known of the *mucous membranes* is, that they are insoluble in water, even by boiling, but are easy of solution in acids, with which they form a pulp.

The *cutis*, by long boiling, is wholly dissolved, forming a solution of gelatin, and by acids and alkalies is easily dissolved into a gelatinous substance. If skin, previously softened, is treated with solution of sulphate of iron, or with oxymuriate of mercury, it combines with the metallic salts; tannin also forms a chemical compound with the cutaneous tissue, which in both these cases ceases to be subject to decomposition.

The *sclerotic coat* of the eye in its chemical properties agrees perfectly with the fibrous membranes, yielding gelatin by boiling. The *cornea* also affords gelatin, but less readily; it swells up in an extraordinary manner when placed in boiling water: in dilute muriatic acid, with the aid of heat, it is dissolved; in acetic acid it swells. The acetic acid in which it has been digested yields a precipitate on the addition of ferro-prussiate of potash, or an alkali, which in the case of the sclerotica does not happen,—a proof, as Berzelius remarks, that the cornea contains also a small quantity of fibrin or coagulated albumen. The vitreous humour belongs to the organised structures; its chemical composition is therefore mentioned here. Berzelius has examined it as taken from the ox; it consists of

Chloride of sodium, with a small quantity of extractive matter soluble in alcohol	1·42
Matter soluble in water	0·02
Albumen	0·16
Water	98.40
	100 00

c. Influence of the nerves on nutrition.

We are still much in the dark concerning the influence of the nerves on nutrition. Affections of the brain and spinal marrow producing paralysis, sometimes appear to leave the nutritive function quite unaffected, although, after the paralysis has endured for a certain time, the part often wastes, and sometimes this effect is produced early. The fact that the nutrition of the limb is not affected in some of these cases, does not necessarily prove that the nutritive function is quite independent of the nerves. In paralysis from lesions of the brain or spinal marrow, the influence of the will over muscular movements, and the transmission of external impressions by the sensitive nerves to the sensorium, are interrupted, but the nerves themselves may still retain their influence; for the power of exciting muscular contractions when the nerves themselves are irritated is preserved for some time although not longer than two months.

In many cases the paralysed parts are wasted and lax; and, what is particularly indicative of the influence of the nerves on nutrition, injuries of paralysed parts are very liable to be followed by gangrene. Schroeder van der Kolk has observed that in some cases the muscular substance is converted into fat, and the arteries ossified.

In the embryo, the nutritive process is remarkably independent of the brain; for the nutrition of anencephalous monsters is by no means defective, and their developement up to the period of birth perfect. But

where any particular nerves have been deficient, the parts corresponding to them have likewise always been absent; and where any organ is wanting, there is always a corresponding absence of the nerves. Tiedemann* has in three cases observed absence of the olfactory nerves coincident with an imperforate state of the cribriform plate of the ethmoid bone and cleft palate. Absence of the eyes is attended with absence of their nerves. Mayer† has described a monster in which the lower extremities were present, with the exception of the absence of two toes on the left foot, but in which the urinary apparatus was absent and the generative organs imperfect; and here the cauda equina was also very imperfectly developed, ceasing abruptly opposite the twelfth dorsal vertebra, while the nerves of the lower extremities were present. In several imperfectly developed monsters the nerves have been said to be wholly wanting; but this assertion may with tolerable certainty be attributed to the difficulty and inaccuracy of the examination. In acephalous monsters which consisted of one extremity merely, a ganglionic nervous mass has been found, from which the nerves of the extremity arose, and which must be regarded as the rudiment of a spinal cord.

The reciprocal dependence of the organs and nerves on each other may be observed very clearly in the metamorphoses of insects, and of the amphibia. Thus, in insects during the metamorphosis, the nervous system undergoes a change of form which has an exact relation to the organs of the creature in its future state; in the caterpillar the ganglia of the nervous cord are nearly uniform, corresponding with the segments of the body; but during the metamorphosis, when individual parts of the body are more developed, and the legs and wings are formed, several ganglia become united into larger masses, opposite the points where the new organs are developed.‡

During the transformation of the larva of the frog, the tail disappears, and with it the extremity of the spinal cord, while simultaneously with the appearance of the extremities their nerves are developed.

This reciprocal dependence of the organs, and of the nerves, on each other for their existence, must not induce the belief that the production of the organs depends on the pre-existence of the nerves. This is by no means the case; both organs and nerves are produced by one and the same power, the nisus formativus, which resides undivided in the germ. When once the organs are formed, however, their constant renovation seems really to depend on the influence of the nerves. Several species of animals, even in their fully developed state, reproduce parts which are lost. The extremities, gills, lower jaw, or eyes, may be removed from the larva of the salamander, and will be reproduced. In this case it is uncertain whether the vital organising principle which exists in all parts of the animal regenerates these parts, in the same

* Zeitschrift f. Physiol. i. 76. † Tiedemann's Zeitschrift. ii. 41.

‡ Herold, Entwickelungs-geschichte des Schmetterlings. Cassel. 1815.

way as in the first developement of them; or whether the central parts of the nervous system which are uninjured by the lesion, effect the reproduction of the parts to which they send nerves. The reproduction of the extremity in the salamander is said to be prevented by the nerve being divided a second time above the surface of the stump. (?) [That this is not always the result, is proved by the following interesting experiment which Dr. Sharpey has kindly given the translator permission to mention. On the 13th of July a considerable portion of the spinal cord at the root of the tail was carefully removed, together with the arches of the vertebræ; the point of the tail was then cut off. The tail was quite paralysed. Reproduction of the part of the tail which was lost, has, however, proceeded as in other cases in which the spinal cord was not injured above the wound; and at this time, August 24th, the newly formed portion of the tail is at least one-fourth of an inch in length.]

It might be urged, as an argument against the nerves exerting an influence in nutrition, that bones are reproduced although they have no nerves; but the nutritious vessels of the bone may, like other parts, be supplied with minute branches from the sympathetic system.

There are few experiments on record calculated to determine in a direct manner the influence of the nerves on the action of the small vessels. Magendie* observed that emetics injected into the veins produced inflammation of the lungs and stomach, but that these effects were much less in degree when the nervi vagi had been previously divided. Magendie remarked likewise that, after division of the fifth nerve, strong stimulants excited no inflammation in the eye; but that after a few days inflammation, with exudation into the interior of the globe, came on even when no irritants had been applied. Dupuy has seen inflammation of the eye ensue after removal of the superior cervical ganglion of the sympathetic, and Mayer has remarked the same occurrence after tying the sympathetic nerve.† Schroeder‡ performed the following experiment. He divided the ischiadic and crural nerves of one leg in a dog, and made a wound in both feet. On the following day the wound of the paralysed limb was dryer than that of the sound limb; during three weeks the wound of the sound foot presented much more violent phenomena of inflammation,—suppuration and granulation took place in it: in the wound of the paralysed foot there was scarcely any inflammation; it discharged a white matter which formed a crust; the wound itself was pale.

I have only once among several cases in which I divided the ischiadic nerve in rabbits for the purpose of investigating the reproduction of nerves, observed that the skin of the heel of the paralysed limb gave way and ulcerated at the part on which the animal rested.

To the influence of the nervous system on the action of the capillaries,

* Journ. d. Physiol. iv. 176. 304.
† Gräfe u. Walther's Journ. x. 3.
‡ Observ. Anat. Pathol. 1826. 14.

may also be referred the sudden changes observed in the condition of wounds after violent affections of the mind. Vering and Langenbeck* have observed that wounds under such circumstances often suddenly lose their favourable aspect.

There is no fact to show that the sympathetic nerve has a more especial influence on nutrition than the cerebro-spinal nerves, except perhaps that the nutrition of a part does not cease when the nerves which it receives from the brain or spinal marrow are divided.

CHAPTER II.

OF GROWTH.

The growth of the solid parts of organic beings is effected in two ways. It may be either interstitial, each of the small particles of the tissue contained in the meshes of the capillary network being enlarged, while the number of vessels are increased, which is the mode of growth of the organised vascular parts; or it may be effected by the apposition of layers of new matter, which is secreted by an organised matrix, the parts that acquire an increase of bulk in this manner not being themselves organised.

a. Of the growth of organised parts by interstitial deposition.

The formation of vessels seems in all parts to be among the first acts of the organising power. Thus in the fibrin effused in the process of inflammation, and in that exuded by the uterus after conception, vessels are formed under the influence of the vital action established between the matter effused and the surface which exudes it. The fibrin contained in solution in the blood, is the only organic matter which possesses the vital property of becoming organised when effused from the vessels, if it is in contact with an organised surface. The first formation of vessels, and their increase, may be observed in the germinal membrane of the egg. The developement of the germinal membrane, and the formation of the canals for the blood in the granular matter which is contained between the serous and mucous layers, between which the heart itself as well as the great vessels are developed, have been described at page 146. The gradual formation of the coats of the vessels in these canals has been admirably demonstrated by C. F. Wolff.† The islets of granular substance enclosed between the reticulated canals, first become transparent in their centre, and the denser and more opaque part of the substance between the transparent centre and the current becomes gradually narrowed from the centre outwards by the extension of the transparency. In very young animals,—for example, in very young fishes,—the formation of new currents may, as Doellinger showed, be observed during the growth of the tail. In the very young fish the arterial current terminates at the end of the tail in a venous current without previous division;

* See Schroeder, v. d. Kolk, l. c. p. 28.

† Theorie der Generation. Berl. 1764.

as the tail grows, the number of the vascular loops increases. The simplest way of explaining the formation of new vascular canals would be, to suppose that the organic matter around the original currents attracts from them the fluid parts of the blood which contain fibrin and albumen in solution, and that, at the same time that it becomes saturated with this fluid, it separates like the granular matter of the germinal membrane into solid islets and intervening canals. The formation of new vessels likewise in the fibrin effused in inflammation may be most easily imagined to be effected by a similar process;—the liquor sanguinis effused condensing on the surface may be conceived to attract through the permeable coats of the vessels more liquor sanguinis, which becomes distributed in the canals formed during the coagulation of the fibrin previously effused; the canals in the fibrin enlarge, and at a later period blood is received into them. The prolongation of the ends of the vessels into the new matter is an absurd idea, particularly as there are no vessels which terminate by open or free extremities; all anastomose with each other, the arteries with the veins by the intervention of capillaries.*

The view here suggested of the formation of new vessels is not, however, consistent with the observations of Doellinger, who has described two modes in which new vessels are formed. 1. By the arterial currents forming for themselves new lateral passages in the growing substance. It is, however, improbable that the particles of the blood force such new ways for themselves, and then accidentally come upon a venous current again. It must still be explained how the new currents arising from an arterial current open into a venous current, in which indeed lies the great difficulty of the subject. Unless we suppose new canals to be formed by the imbibition of liquor sanguinis into the substance of the part between the arterial and venous currents, and by the separation of the substance into canals and islets, it is very difficult to conceive how the new currents can find means of terminating in the already existing venous currents; for if such canals did not previously exist, the blood would accumulate in the parenchyma rather than form regular capillary loops. 2. A second mode of production of new currents, described by Doellinger, is the following:—A line of fixed animal matter near a current of blood is set in motion; a moveable column, as it were, is formed out of what Doellinger denominates mucous granules, (Schleimkörner,) which by one extremity nearly joins the current of blood at a right angle, while its other extremity is directed from it. This tract of matter moves to and fro—towards the current of blood, and from it—with a pulsatory motion; the granules composing it, arrange themselves in a line and gradually assume a more defined form, becoming distinctly oval; the oscillating mass at last divides into two currents, of which the one takes an arterial, the other a venous

* An accurate account of all the observations on this subject is given by Dr. Allen Thomson in Jameson's New Phil. Journ. No. 18, 19, and 20.

course. I confess that I cannot think this to be the usual process in the production of new currents. The oscillation of the column of matter described by Doellinger, either is derived from the impulse of the arterial current, or it is not. If it is not connected with it, the union of the oscillating column with the current is as difficult to conceive as the union of two currents in any other case. If the oscillation is derived from the arterial current, and if the current of oscillating matter returns to the point from which it arose, a loop-shaped offset from an artery is formed, but not a new loop between an artery and vein. The new vessel can, however, be of the former kind only in the case which Doellenger instances, namely, at the extremity of the arterial trunk in the tail of young fishes, where the artery inosculates directly with the venous trunk, being reflected as it were into it; or perhaps also at the extremities of branchial lamellæ, where likewise the arterial current is reflected into the venous. Meyen* has in fact observed that in the branchiæ of the young larva of the salamander, the arterial current sends out a small twig to each lateral division of the branchial lamella, and that the blood globules returning from the divisions of the lamella enter the same arterial current from which the branch arose. At a later period, however, this ceases to be the case; the artery of each branchial lamella arises from the arterial trunk of the axis of the branchia; the vein of each lamella returns not to the artery, but to the corresponding vein of the branchial axis. In animals generally also the small vascular loops are not offsets from one vessel, but form an anastomosis between an artery and a vein. It requires further observations on the branchiæ of the salamander larva, and on other parts, to decide whether the theory of the formation of new vessels, which I have advanced above, but which at present is not supported by sufficient observations, is not in many cases consonant with the process pursued by nature.

The growth of different parts of the body has hitherto been little investigated. It is probable that in all parts the mode of growth is essentially the same, consisting in the increase of the elementary particles of the tissue in the spaces enclosed by the capillary currents, sometimes in number, as in the case of fibres of muscles and nerves,—sometimes in size, each particle in the meshes of the network assimilating to itself more nutritive matter, while at the same time the number of capillary vessels increases in equal proportion with the volume of the solid tissue.

Structure of bone.— Before treating of the growth of the bones, it is necessary to premise a few remarks on their structure. A very good investigation of the minute structure of the bone,—the first for a long period which has afforded any really new results concerning this subject,—has been instituted by Deutsch,† under Purkinje's direction. The bone having been previously freed from its earthy matter by maceration in

* Isis, 1828. Tab. vi. fig. 3.

† De penitiori ossium structurâ observationes. Dissert. inaug. Vratisl. c. tab. i.

dilute acid, thin sections of it were submitted to observation with the microscope. In very thin transverse sections of long bones the circular openings of the longitudinal canals are seen; in longitudinal sections these canals are seen divided longitudinally; they contain medullary matter, and only here and there communicate with each other. In the spongy bones these medullary canals are replaced by cells. The results of Deutsch's observations on the more intimate structure of the cartilaginous substance of the bone are perfectly new. In the transverse sections (plate I. fig. 10) there are seen, surrounding the mouth of each canal, fine concentric lines, which, on examining the longitudinal sections (plate I. fig. 11), are perceived to be lamellæ surrounding the canals, and running their whole length. The diameter of these lamellæ is $\frac{1}{480}$ of a line. The spaces in the transverse section of the bone, which are not occupied by the longitudinal canals and their concentric lamellæ, are filled by other lamellæ, which form larger concentric rings around the great medullary cavity. In the flat bones of the cranium and other flat bones, the canals, with their lamellæ, run parallel with the surface of the bone. It is very remarkable that the thickness of the lamellæ is traversed by numerous lines which are separated by very small intervals, and which correspond in length to the thickness of the lamellæ, namely, $\frac{1}{480}$ of a line. Deutsch supposes these lines to be tubes in which the calcareous matter of the bones is deposited (?); if one lamella is separated from another, the ends of the lines are seen, he says, of a triangular form. The existence of these fine tubes (?) was hitherto quite unknown; but it is not probable that they serve for the reception of the calcareous matter, for the first appearance of ossification is in the form of a microscopic network. Purkinje has discovered, in the cartilage of bone, roundish corpuscules, which are much larger in diameter than the transverse sections of the last described tubes. These researches on the lamellar structure of the cartilage of bone have been repeated by M. Miescher, in the anatomical school of Berlin, and found nearly entirely correct. The corpuscules have been found by Miescher, also, in cartilages which do not become ossified, and even in the callus of fractured bones. The cartilages of the ear and those of the trachea form the only exceptions, and consist of cellular cartilage.

[The circular canals in the bone, described by Deutsch, are identical with the longitudinal and transverse pores of Havers,* and also with the third and fourth kinds of tubes described by Leeuwenhoeck.† The third kind of pores, Leeuwenhoeck says, are disposed in a definite order, and are surrounded by concentric circles. The fourth kind of foramina were the larger and more rare openings of the same kind. Both the canals

* Osteologia Nova, 1691.

† Anatomia s. interiora rerum ope micros. detecta. Lugd. Bat. 1687, p. 199, as quoted by Miescher, vide infra.

and the corpuscules of Purkinge have, as Miescher* observes, a brown ash colour. The canals are continuous with the cells of the flat bones, and with the medullary cavity of long bones; the cells, like the canals, are surrounded with concentric layers, and both cells and medullary canal are to be regarded as enlarged canals of Havers, while the canals, on the other hand, contain a medullary matter, in which run blood-vessels that are derived as well from the external surface of the bone as from the medullary cavity. The diameter of the Haversian canals varies, according to Miescher, from $\frac{1}{320}$ to $\frac{1}{828}$ of an English inch. Miescher does not confirm Deutsch's statement as to the still more minute tubes traversing the concentric lamellæ, although he perceived a radiated appearance around the larger canals, which was produced by dots or short lines, which do not occupy the whole thickness of each lamella. This appearance the translator has endeavoured to represent in fig. 12, plate I. Some of the lines appear to traverse more than one lamella, though the majority, as Miescher describes, are very short. They appear more like the separations between the granules of cartilage that form the lamellæ than distinct tubes.

The corpuscules discovered by Purkinje are supposed by Miescher to be the brown spots which Leeuwenhoeck observed, and which constitute his second order of foramina. In bone deprived of its earthy particles by maceration in acid, their appearance is that of small brown spots, pellucid in the centre, and surrounded with a distinct opaque line, which, by a high magnifying power, appeared to Miescher to be denticulated. They are ovate in form, more or less compressed, and pointed at the extremities. They are situated between the lamellæ, their long diameter being oblique with regard to the direction of the lamellæ. According to Miescher's measurement, their long diameter is from 0·0048 to 0·0072 of a line the short diameter from 0·0017 to 0·0030. By examining very thin lamellæ of bone from which the calcareous matter has not been extracted, with a very powerful microscope, Professor Müller has perceived, that, from the flattened surface of the oval corpuscules, a number of lines, which he believes to be very minute tubes, arise, traverse the lamellæ of the pellucid substance, and unite with the tubes from other corpuscules. The diameter of these minute canals varies, he says, from $\frac{1}{5000}$ to $\frac{1}{3333}$ of an English line. When viewed as opaque objects upon a dark surface, both the canals and corpuscules appear white; when seen by transmitted light they appear opaque, while the surrounding substance appears transparent, see fig. 13, plate I. They present the same appearance in natural thin laminæ of bone which have not been ground, such as those of the ethmoid bone of different animals. Their white colour and opacity are not altered by heat or by boiling in alcohol or ether. In bones affected with mollities, in which disease the calcareous matter is deficient, these white opaque corpuscules and their tubules are no longer

* De inflammat. ossium, eorumque anat. general. dissert. Berlin, 1836.

visible. On the contrary, in fossil bones, and in bones from which the animal matter has been removed by boiling with carbonate of potash, they are still evident. If thin laminæ of fresh bone be acted on by muriatic acid, the corpuscules and tubes become pellucid like the intervening substance. From these observations Prof. Müller infers that the corpuscules and their canals contain calcareous salts, either in their interior or in their parietes. But he admits that they do not contain all the earthy matter of bone; for in some fishes, as in the esox lucius and others, they do not exist; and when bones are burnt, or treated with a boiling solution of carbonate of potash, they yield much more calcareous matter than could be accounted for by the corpuscules and tubules. They preserve their form also, which would not be the case if merely these scattered corpuscules and delicate tubes remained. The intervening substance, which constitutes a larger part of the bone than the corpuscules and tubules, assumes a white colour when the animal matter is removed by the action of carbonate of potash, and has then a granular appearance. Prof. Mayer has recently suggested that the corpuscules are merely red particles of the blood impregnated with calcareous matter, and that the appearance of ramifying canals described by Prof. Müller arises simply from the separation of the granules of the amorphous osseous substance during desiccation. The representation, fig. 13, plate I. copied from Prof. Müller's paper, corresponds exactly with what the translator has seen, by transmitted light, in thin sections of the bone, both of mammalia and of the common fowl: but he is rather inclined to adopt Prof. Mayer's opinion regarding the ramifying lines; although not having viewed the bone as an opaque object on a dark surface, as Müller directs, he cannot speak with confidence on the subject.]

The growth of bones takes place chiefly on the surface, and at the extremities of the diaphysis, by the deposition of new layers of cartilage which are organised and become ossified. This mode of growth is evident; the bones enlarge externally, while osseous matter is absorbed from the interior, so as to give rise to the medullary cavity.*

Duhamel placed a ring of silver wire around one of the long bones of a young animal, and after some time found that the ring enclosed merely the medullary cavity,—the bony substance which it had before surrounded having disappeared. The bones undergo constant change even to the period of extreme old age, when the cranial arch becomes thinner in consequence of the partial absorption of the diploe. When animals are fed with rubia tinctorum or madder, which has a great affinity for phosphate of lime, and therefore colours principally the bone and teeth, the whole tissue of the bones is reddened. In young pigeons this universal

* The various facts relating to this subject will be found in the first volume of Prof. E. H. Weber's excellent edition of Hildebrandt's Anatomie; and in the Dict. des Sc. Med. art. Osteog. t. xxxviii.

reddening of the bones takes place, according to Morand and Gibson, in a single day; the old bird requires to be fed with madder fourteen days before the bones acquire a rose colour. The growth appears, nevertheless, to take place principally at the surface and ends of the bones. Duhamel having fed animals on madder for a certain period, then omitted it for a time, and afterwards resumed its use, found, on killing them, that the bones presented alternate layers of red and white substance; in young animals, however, the bones were generally found reddened throughout. If the bones were examined while the animal was being fed on the madder, the most external layer of bone was found red. From these experiments Duhamel, although he admitted the interstitial growth of bone, concluded with Grew, that the osseous substance was formed principally by the deposition of layers on the surface, like the layers of wood in trees. This is, however, by no means certain; for in Morand's experiments the bones of full-grown pigeons became red throughout, and it was observed by Duhamel himself that the bones of a cock became red in their whole thickness in sixteen days, those of a pigeon in three days.*

The long bones grow principally at the line of separation between the already ossified portions of the bone and the cartilaginous portion, which, in childhood, still exists between the shaft and epiphysis of the bone. This seems to be proved by that experiment of John Hunter, in which he bored two holes at the extremities of the middle ossified portion of a long bone of a young pig, and after some months found the distance between the two holes not increased, so that the growth must have taken place principally in the portions of bone beyond these perforations.† The growth of the long bones in length, therefore, continues only so long as the epiphyses and shaft are divided by a layer of cartilage.†

The bones are, in the fœtus, at first cartilaginous, and originally contain no cells and medullary cavities. The cells of the bones are for a long period absent, but are in part developed before the cartilaginous substance becomes ossified by the deposition of an increased quantity of phosphate of lime. The ossification commences from separate points, from which the osseous lamellæ or fibres proceed; in the flat cranial bones, in a radiated form. Ossification commences as early as the second month of uterine gestation.

[Miescher,‡ by the use of a good microscope, has been enabled to add to our knowledge of the process of ossification. He shows that in a thin lamina, taken from a longitudinal section of the femur of a fœtal rabbit, the part not ossified consists of a pellucid colourless cartilage, closely interspersed with oval brownish corpuscules, the longest

* See Gibson, Manchester Memoirs, New series, vol. i.; and in Meck. Arch. iv. 482.

† [The bone, showing the result of this experiment, as well as bones of animals fed on madder, may be seen in the museum of the College of Surgeons, Physiological series.]

‡ Loc. cit.

diameter of which is transverse. Near the middle ossified portion of the shaft of the bone the cartilage is more transparent, and the corpuscules more separate. The ossified part of the bone is more opaque; at its margin the corpuscules of the cartilage are partly surrounded each by a dark line, forming the segment of a circle, open towards the cartilaginous parts; within this margin the dark circles are complete, and thicker, so as to embrace more and more closely the corpuscules the nearer they are situated to the centre of the ossified part, where the bone is very opaque and its texture obscure. Miescher found that when the osseous matter was removed from a portion of ossified bone by the action of muriatic acid, the corpuscules were left apparently in the same state as before.

The process of ossification in the epiphysis is rather different from that in the shaft of the bone. The corpuscules in the part of the epiphysis most distant from the ossified portion are very close to each other, and not disposed in any order. Nearer the line of ossification they are seen to be arranged in single or double lines, running with more or less regularity perpendicularly to the ossifying surface, the long diameter of the corpuscules forming the lines being always transverse. Still nearer to the ossified bone they appear larger in size, and are more distant from each other, and the cartilage between them is rather more opaque. (See fig. 14. Plate I.) Lastly, opaque striæ are seen stretching, like the teeth of a comb, from the surface of the bone into the cartilage that separates the lines of corpuscules. At their base these striæ are united to each other, and behind them are oblong spaces containing corpuscules, and inclosed by similar opaque lines of ossification; the cartilaginous matter, also, between the corpuscules in these spaces loses its transparency, and thus the primary osseous tissue is formed, the canals of Havers and the cells being formed in this tissue at a later period. A transverse, or slightly oblique section of an ossifying epiphysis presents corresponding appearances. (See fig. 15. Plate I.) In the part not yet ossified the corpuscules are scattered without order; then they are seen collected into groups of two or three, at nearly equal distances, in the transparent cartilage; at the line of ossification the groups are surrounded by opaque rings, forming a network; the rings become thicker and thicker, while the cartilage between the included corpuscules also becomes opaque, and the texture at last indistinct; the original appearance is, however, restored by the action of acid. The appearances presented by the ossifying cartilage of the epiphysis, described and represented by Miescher, were observed several years ago by Dr. Sharpey in the bones of the fœtal calf, but not published. The figures 14 and 15, plate I. are copied from drawings, for the use of which the translator is indebted to Dr. Sharpey's kindness, and which were made at Edinburgh, under his direction, by Dr. Allen Thomson

in the year 1830. Dr. Sharpey has, likewise, drawings made at the same period, which represent beautifully the process of ossification in the parietal bone of the fœtal calf. The osseous substance is represented radiating in a branched form from the centre of the bone, and the osseous corpuscules, since described by Purkinje and Deutsch, are clearly shown scattered through it.

The translator has observed, that, if the cartilage is cut transversely at the part where the corpuscules are arranged into groups or columns, the groups themselves are seen to radiate from different centres, which are sections of canals in which blood-vessels run. The translator has represented this appearance at fig. 16, plate I. It is interesting, as indicating the relation that exists between the changes in the cartilage preceding ossification and the blood-vessels. The cartilage between the columns of the aggregated corpuscules at the ossifying surface is very transparent, and apparently dissolved in part; at all events, its nature is so changed that the epiphysis separates, with the greatest ease, from the bone at the line of ossification.]

The coccyx, patella, and most of the bones of the carpus and tarsus, are not ossified till after birth.*

It is quite an erroneous notion to imagine that one organised part may be the nutrient organ of another; for instance, that the substance of the bones is formed and nourished by the periosteum. The osseous substance, being itself organised, must itself assimilate the nutritive matters. It is only the unorganised parts,—parts which have no vessels,—such as the hair, nails, teeth, and crystalline lens, (?) that are produced by an organised matrix, and maintained by the mere apposition of new matter. The idea that bones are formed by the periosteum, appears to me to be a barbarism unworthy the present state of physiology. The bones receive their vessels from the periosteum and from the medullary membrane; they die, therefore, when either of these membranes is destroyed to any considerable extent; when the periosteum is destroyed, the outer layers perish,—the inner layers when the medullary membrane is destroyed. But it does not follow from this, that these membranes deposit the calcareous matter in the bone. The periosteum is simply the means of transmission of vessels to the bones; the death of the bone, when the periosteum is destroyed, arises, therefore, from its vessels being torn asunder.

Growth of muscles and nerves.—Concerning the mode of growth of the primitive fibres of muscles and nerves, we are quite in the dark. It is not known whether the number of muscular fibrils remains the same throughout life from their first formation, their only increase being in length and thickness; or whether their number also increases during

* The developement of the osseous system will be treated of in the eighth book.

growth as the effect of exercise. To determine the question, accurate microscopic admeasurements of the diameter of the fibres of muscles and nerves must be made at different ages, of the diameter of the nervous fibres in cases of atrophy of the nerves,—for instance, of the nerves of the cauda equina in the case of tabes dorsalis. The investigation of this subject has been commenced by Valentin * in his interesting paper on the evolution of the muscular system. He describes the muscles in the very young embryo to consist of distinct globules which afterwards disappear, a uniform cylindrical fibre appearing in the place of a thread of globules like pearls. He finds the fibres in the young embryos of mammalia and birds to be always thicker than in the more fully developed animals. The first beaded fibres he describes as three times or more thicker than the muscular fibres of the embryo further advanced in developement, so that it would appear that from each of the original fibres several were afterwards formed. The primitive fibrils of muscles and nerves being so small that the capillary vessels do not enter them, but merely ramify in the spaces between them, we must suppose that their growth is effected by the attraction and assimilation of the fluid parts of the blood.

The mode of the original formation and growth of the *glandular canals* in the fœtus will be described in the chapter on the intimate structure of the glands, in the third section of this book.

The question, in what parts interstitial growth is the mode of increase, and in what parts it is not, is identical with the question as to what parts are organised or contain blood-vessels. The tendons, ligaments, and cartilages have blood-vessels, although in small number. In the museum of Fremery of Utrecht, I saw a very beautiful injection of the costal cartilages, and of the cartilages of the larynx and trachea (if I recollect aright, from a young fox). Of the vessels of the cornea, vitreous humour, and serous membranes, I have already spoken.† The existence of vessels in the internal membrane of the blood-vessels is still doubtful.

b. Of the growth of unorganised non-vascular parts by the successive deposition of layers of new substance.

Unorganised non-vascular parts are produced by an organised matrix, and grow by the continued deposition of new matter on one surface. Their matrix is in some cases a plane surface, in others a projecting one, and again in another instance a closed sac. To these different varieties belong, 1. the horny tissues; 2. the teeth; and 3. the crystalline lens.

In the lower animals the shells are also formed by the secretion of successive layers. The form of the shell of molluscous animals depends altogether on the form of their body, and of the surface which secretes

* Historiæ Evolutionis Syst. Muscul. Prolusio. Vratisl. 1832. † See p. 215.

the shell, which consists of carbonate of lime mixed with an animal matter. In the shell of the muscle the small external lamellæ are first formed, the large internal ones last. Bournon has discovered that the carbonate of lime in these layers has a crystalline arrangement which can be perceived by the microscope.

1. *Of the horny structures.*—To the horny structures belong the epidermis of the skin, the epithelium of the mucous membranes, the hairs, spines,* nails, claws, hoofs, horns, and feathers.†

a. Epidermis and Epithelium.—The epithelium of the mucous membranes is most distinct in the mouth, less so in the œsophagus. It is very distinct in the gizzard of granivorous birds, where it presents horny plates, and in the upper half of the stomach of the horse. In the intestinal canal it seems to be extremely delicate, and can only be distinguished in the form of the friable unorganised investment of the villi which I have described in the note at page 268; it here approaches very nearly the nature of mucus. The skin of the amphibia, which secretes a mucus, is also provided with an epithelium. Wagner speaks of this being cast, and I have myself seen the cuticular covering which the larva of a salamander had thrown off. It is difficult to conceive how the mucous membranes can secrete mucus and epithelium at the same time, unless we suppose that the mucus is secreted by the follicles dispersed through the mucous membranes, and the epithelium by the surface of the membrane in the intervals. In some extensive tracts of mucous membrane, the formation of the epithelium seems to be allied to mucus, as in the small intestines; and many mucous membranes in which there are no mucous follicles, such as the lining membrane of the maxillary, frontal, and sphenoidal sinuses, and the conjunctiva of the eye-ball, seem to secrete mucus merely, so that follicles would appear not essential to the formation of mucus.

The cuticle, or epidermis, consists of horizontal lamellæ which can be distinctly shown, at least in the cuticle of the palm of the hand and sole of the foot, particularly by the aid of boiling. The most internal layer of the epidermis is still soft, and is commonly called the rete mucosum

* On the structure and growth of spines, consult Boeckh, De spinis histricum, Berol. 1834; Müller's Archiv. 1835, p. 236; the first edition of Müller's Handbuch der Physiol. p. 368; [and the Catalogue of the Museum of the College of Surgeons, Physiol. series, Tegumentary system.]

† The developement of feathers has been studied by A. Meckel, Reil's Archiv. 12. 37; Dutrochet, Journal de Physiol. 88. 333; and Fr. Cuvier, Froriep's Notiz. 317; Mémories du Muséum, t. xiii.; [also by Hunter; see the Catalogue of the Museum of the College of Surgeons. An account of the structure and growth of feathers will be found in the Cyclopædia of Anat. art. Aves, by Mr. Owen. The account of the observations of Meckel and M. F. Cuvier, given by Prof. Müller in the text, being scarcely intelligible without illustrations, has been omitted by the translator.]

of Malpighi. The cuticle of the negro is blackish, particularly its most internal layers. The organised texture which secretes the epidermis is white even in the negro.* It is not ascertained with certainty whether the cuticle is continued into the sockets for the hair-bulbs, and into the sebaceous follicles, or how far it extends into them. When the cuticle is removed, no pores have been observed by most observers; but, even if they did exist, they would not be visible any more than punctures in caoutchouc.

Eichhorn and Lauth describe it to be continued into the hair follicle as far as the point where the hair is attached, and assert that, on removing the epidermis from the cutis, such sheaths are often visible. Eichhorn says, that the holes through which the hairs pass can be seen in the epidermis separated from the skin, by looking in an oblique direction.

[Gurlt also has shown that the epidermis is really continued into the perspiratory canals, as well as into the follicles for the hair. In animals in which the cuticle is coloured, he was able to trace it by its colour for some distance into these parts.]

The perspiratory pores will be described in the section on secretion.

The cuticle is secreted in successive layers by its matrix, the most superficial layer of the cutis.

[M. Breschet has described peculiar organs for the secretion of the epidermis, and calls them the blennogenous organs. A description and a representation of them will be given in the section on secretion.]

When in inflammation of the skin, such as that produced by a blister or a burn, the cuticle is raised from it by the serum secreted, it is reproduced; in the inflammation of the skin also which occurs in the exanthemata, the cuticle is lost by desquamation, and is then also reproduced. In man and mammiferous animals it is constantly falling off in minute scales, in reptiles it comes off entire at the time of the so-called casting of the skin, in insects in the larva state before their transformation, and in spiders the same thing occurs. In some snakes the eye is completely covered in by the cutis which is invested on its inner surface by the conjunctiva, so that the eye-ball moves free behind it; and here the cutis covering the eye secretes epidermis externally, which comes off with the rest of the cuticle when "the skin is cast." In the tortoises and crocodiles the cuticle in several distinct places assumes the form of thick plates of horn consisting of lamellæ. Under the horny plates on the back of the crocodiles, there are plates of bone—parts of the dermal skeleton,—which are organised. In some lizards, likewise in the iguana and blind-worm, for instance,—the scales, which are often quite hard, are not mere horny plates, but contain harder organised bodies which secrete

* E. H. Weber in Hildebrandt's Anat. i. 187. See also Seiler in Pierer's Med. Realwörterbuch. Integumente.

the horny substance in thin lamellæ on their surface as a kind of epidermis.

The callosities of the human skin arise from the cuticle being formed in layers thicker than natural. In corns and warts, however, and in icthyosis, a part of the organised cutis itself seems to be converted into a horny substance.

The cuticle even of the living body swells when macerated in water; it undergoes no further change when boiled. It is gradually dissolved by concentrated sulphuric acid, and very readily by alkalies; nitrate of silver gives it a grey colour, which afterwards changes to blackish. The long continued internal use of nitrate of silver produces the same effect, which results from the silver uniting with the sulphur of the animal matter so as to form sulphuret of silver. Tannin, which in the process of tanning combines with the cutis, does not unite with the epidermis.

The epidermis is formed in the embryo as early as the second month.

b. Nails, claws, hoofs.—The manner in which the nails are formed is not yet so clearly made out as could be wished. They are inserted by their posterior border or root into a groove in the cutis, which is beset with papillæ, and the surface of the cutis on which the inner surface of the nail lies is also beset with papillæ arranged in longitudinal rows. The white colour of the nail near its root, and the red colour in the rest of its extent, arise merely from the different colour of the cutis at these parts. Professor M. Weber* and Lauth† have described the cuticle to be continued under the nail to its posterior border, and to be also attached to its upper surface along the same posterior border. According to Lauth, the substance of the nail is secreted partly by the cutis on which it rests, and partly, in larger proportion indeed, by the bottom of the groove in which it is inserted, so that it is increased in thickness at the same time that it is thrust forwards by the apposition of new matter to its root. But it is difficult to reconcile with this the continuation of the cuticle under the nail, forming, according to Lauth's idea, the innermost layer of the nail. Further examinations must decide whether the papillæ of the groove in which the root of the nail is fixed, do not alone secrete the whole thickness of the nail; the under side of the nail, in that case, being merely agglutinated to the fresh layer of epidermis secreted under it.

[Gurlt confirms the statement of Weber and Lauth as to the existence of a very thin layer of epidermis beneath the nail, which, he says, is distinct in some domestic animals. The microscopic examination of thin perpendicular sections of nails cut longitudinally, disclosed fibres running from the upper surface forwards, and towards the under surface, and in-

* Zergliederungskunst, i.

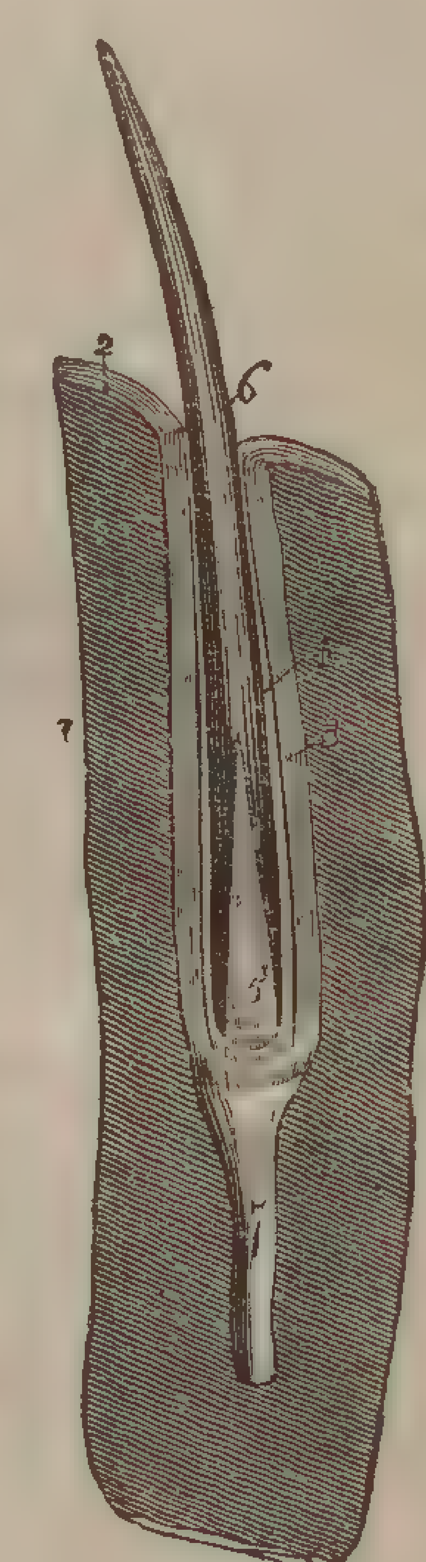
† Mem. sur divers points d'Anatomie, and in his Manuel de l'Anatomiste, p. 303.

termingled with these fibres numerous point-like bodies. Gurlt supposes, therefore, that the horny matter at first fluid, is secreted both by the cutis in the groove in which the root of the nail is fixed, and by that of the surface which the nail covers, and that the secretion of the latter part chiefly determines the thickness of the nail.]

Diseased crooked nails evidently consist of imbricated lamellæ lying one upon another, and directed, from behind and above, forwards and downwards. In hoofs the horny substance is not secreted by a furrow in the skin, but by a determinate portion of the surface of the phalanx.* The nails, according to J. F. Meckel, are first formed in the fifth month of fœtal life.

Fig. 25.§

Fig. 26.||



c. Hairs.—The hair is formed in the hair follicle—an elongated sack, to the bottom of which the hair is fixed by the bulb, or that portion of the hair which is still in a soft state, (fig. 25 and 26.) Several observers, as Heusinger† and Eble,‡ describe two substances in the hair; a solid uniform cortical substance, and an internal more cellular substance. Heusinger rested chiefly on the hair of the roe-deer as a proof of the cellular structure of the internal substance. In the quills or spines of hedgehogs and porcupines, which are different from hairs, the two substances are distinctly observable. In transverse sections the internal spongy substance has a radiated appearance. The bristles of the hog are, according to Eble, formed of an internal cellular substance, and a cortical portion constituted of fibres which can be easily separated. E. H. Weber finds the human hair to consist of a perfectly homogeneous substance, in which no distinction of cortex and medulla can be perceived. He finds them, moreover, to be for the most part flattened and excavated on one side, so that the transverse section is reniform; this is certainly the form of the hair of my own head. The hair of the bat is knotted; that of grey animals, such as the

* On the structure of hoofs and claws, consult Heusinger, Syst. d. Histologie, i.

† Syst. der Histologie, Eisenach, ii. 1823.

‡ Die Lehre von den Haaren. Wien, 1831.

§ [Pulp of a hair injected, after Hunter, in the Catalogue of Museum of the College of Surgeons.—1. Cut surface of hair; 2. the pulp; 3. injected vessel ramifying in it.]

|| [Whisker of a walrus in its follicle, after Hunter, in the Catalogue of the Museum of the College of Surgeons.—1. Cut surface of lip; 2. cutis; 3. external sheath of the follicle; 4. internal sheath continuous with the cuticle, which, both in the drawing and in the preparations which Mr. Hunter has left, is seen to line the follicle to the point of attachment of the bulb of the hair; 5. pulp ormatrix; 6. shaft of the hair; 7. large nerve going to it.]

mouse, is mottled with black and white. For an account of the many varieties in the structure of the hair, I must refer to Heusinger's excellent description and plates. Heusinger and Eble have very accurately examined the origin of the whiskers of carnivorous animals. The hair commences at the bottom of the follicle, by a swelling called the root or bulb of the hair (fig. 26); it is softer than the hair, and is always distinguished by its white colour; it is hollow, and contains within it the pulp of the hair, which is probably a vascular prolongation of the bottom of the follicle, (see fig. 25). Heusinger describes a continuation of the epidermis as lining the sheath. The pulp, according to these anatomists, is longer in these vibrissæ or whiskers, than in other hairs. Eble has proved, by minute injection in the cat, that the sheath of each of these hairs is very vascular, and even the pulp of the hair was reddened by the injection, though no distinct vessels could be traced into it. In the follicle of the human hair Eble has not succeeded in demonstrating the soft sheath. The bulb of the hair in man consists of the soft part of the hair and the pulp within it. The bulb is club-shaped, and thicker than the rest of the hair. The pulp is gradually lost in the medullary substance of the hair. From these anatomical facts it appears that the substance of the hair is formed by the secretion of horny matter on the surface of the conical vascular pulp. The hair grows by the addition of new matter at its root or point of attachment; it grows at no other part. The exterior parts of the hair consequently are the first formed. The pulp of hair also has its different stages of developement; and on this depends, of course, the different form of the hair at different parts of its length, as well as the difference of colour which it often presents in animals at different parts of its length. The spines of some animals are also pointed at their extremity, thickest in the middle, and again thinner near their root. As these parts are all formed in succession one after the other, their different thickness can only depend on the different states of developement of the matrix. That changes of a similar kind take place in the pulp of the hair is shown by the not unfrequent occurrence of hairs of which the part near the insertion is thinner than the other part. These stages of developement of the pulp are seen most distinctly, and are most remarkable, in the formation of feathers. Lauth* asserts that the continuation of the epidermis into the follicle as far as the attachment of the hair is very distinct in the whiskers of the fox and otter. The epidermis is continuous, he says, at the bottom of the follicle with the base of the hair, so that the hair is essentially epidermis developed into the form of hair by the active secretion of the conical papilla on which the base of the hair rests. Eble denies the fact stated by Lauth.

In the disease called plica Polonica, the hairs become glutinous on their surface. The bleeding from hairs cut off close to the root in this

* Mém. sur divers points d'Anat. fig. 9. Manuel de l'Anatomiste, p. 302.

disease, if a fact, may perhaps arise from the secreting papilla or pulp being prolonged into the hair. This pulp is in the whisker of the dog so long that a drop of blood flows when the hairs are cut off close to the skin, a fact which Eble has also remarked.

Hairs become electric by friction. By drawing the collector plate of a common condenser once very gently over my head, sufficient electricity was developed to cause the separation of the gold leaves of the electrometer when the plate was brought near it. This property, however, is also possessed by hairs after death.

The account of the *chemical composition* of hairs I shall borrow from Berzelius.* They consist of horny matter. Vauquelin states that their different colours are produced by a coloured fatty matter; and black hair is also partly indebted for its colour to iron,—the sulphate? When the fatty matter is extracted by means of alcohol or ether, the hair assumes a greyish yellow colour; so that the grey colour of hair in old age would seem to arise from the coloured fatty matter not being secreted with the new matter of the hair. Alcohol also extracts osmazome with its accompanying salts,—chloride of sodium and potassium, and some chloride of ammonia,—which, however, Berzelius believes to be derived merely from the perspirable matter adhering to the hair. The horny matter of the hair has the same chemical properties as that of horn. It is not soluble in water, alcohol, or ether, or even in concentrated sulphuric acid. The horny substance, after being softened by maceration in cold nitric acid, is soluble by boiling in water; and the solution, after evaporation, becomes a gelatinous mass on cooling. This gelatinous substance is now soluble in cold water, and is precipitated from it by tannin. The horny matter is readily soluble in caustic fixed alkalies, but perfectly insoluble in caustic ammonia, and is thus clearly distinguished from coagulated albumen and fibrin. From coagulated albumen it is also distinguished by its insolubility in acetic acid, and by uniting with potash to form a saponaceous substance (hornkali.) By boiling in a Papin's digester, Vauquelin effected the solution of the hair in water: the solution contains sulphuretted hydrogen. Chlorine destroys the colour of hair, and afterwards unites with it; a bitter adhesive compound being formed. Epidermis and hair combine with the metallic oxides; are blackened by nitrate of silver, the sulphur of the hair forming, with the silver, sulphuret of silver. Hair melts when heated, and burns with a bright flame, and with the smell of burnt horn; when subjected to dry distillation, ammonia and sulphuretted hydrogen are developed. The ash of the hair amounts to one and a half per cent. of its weight, according to Vauquelin. It contains oxide of iron, a trace of oxide of manganese, sulphate, phosphate, and carbonate of lime, and a trace of silica; black hair contains most iron, light-coloured hair the least;

* Traité de Chimie, t. vii. p. 313.

the latter, however, contains phosphate of magnesia. Hair contains oxygen, hydrogen, nitrogen, and carbon; but in what proportions is not known.

d. Horns.—The antlers of the deer tribe must not be confounded with horns; the former are at one period organised, horns never: the matrix of horns is the surface of bony processes. The frontal horns of ruminating animals are formed by the secretion of successive layers of horny substance on the surface of processes of the frontal bone, the form of which determines that of the horn; the horny laminæ are secreted one within the other, the last formed being, therefore, always the most inferior and most internal, and each new layer has a wider base than the former. The horn of the rhinoceros has no internal matrix like the horns of the frontal bone of the ruminating quadrupeds, but arises from the skin over the nasal bones. The horns of the rhinoceros are therefore solid, and have the peculiarity of consisting of numerous fibres, like hairs, agglutinated together.

2. *Of the structure of the teeth.*—The jaw-bones are sometimes furnished with horny plates, such as the mandibles of birds, and of the chelonian reptiles, and the whalebone lamellæ of the whale; in other cases they are armed with teeth. In neither instance are these organs organised; they are formed by an organised matrix.* The matrix of the tooth is the follicle. The little sacs or follicles in which the teeth are formed lie in the alveolar groove of the jaw of the fœtus covered by the gum. The follicles for the milk teeth are formed as early as the third month of fœtal life; those of the permanent teeth are in part formed before, in part after birth. Each sac consists of two vascular membranes. The internal membrane in its form resembles a mould of the crown of the tooth, which is formed, however, not by the membrane of the follicle, but by the pulp which rises from its base at the part at which the vessels and nerves enter it. (See fig. 27.) The surface of the pulp takes the form of the crown of the future tooth; and about the middle period of uterine life, the secretion of layers of dental substance commences on it in the form of calices corresponding to the points of the crown. These little cup-like plates on the different points of the crown of the tooth are at first separate, but they gradually unite together, and

Fig. 27.†

* On the structure of the teeth, consult Cuvier, Anatomie Comparée, and his Ossemens Fossiles; Heusinger's Histologie; Rousseau, Anat. Comp. du syst. dent. Paris, 1827; Blake, on the teeth, 1801; Hunter, on the teeth, 1803; Blandin, Anatomie du systeme dentaire. Paris, 1836.

† [Representation of the follicle and pulp of a canine tooth, after Hunter:—1. Part of the alveolar process of the jaw; 2. the membranes forming the follicle or capsule; 3. the pulp; 4. first formed portion of the tooth resting on the summit of the pulp.]

the soft crown of the pulp of the tooth is then inclosed at the upper surface and sides by a shell of dental substance. [See fig. 28, which is copied from Blake, and illustrates the gradual formation of a molar tooth.] This shell, which is the outermost layer of the osseous substance

Fig. 28.

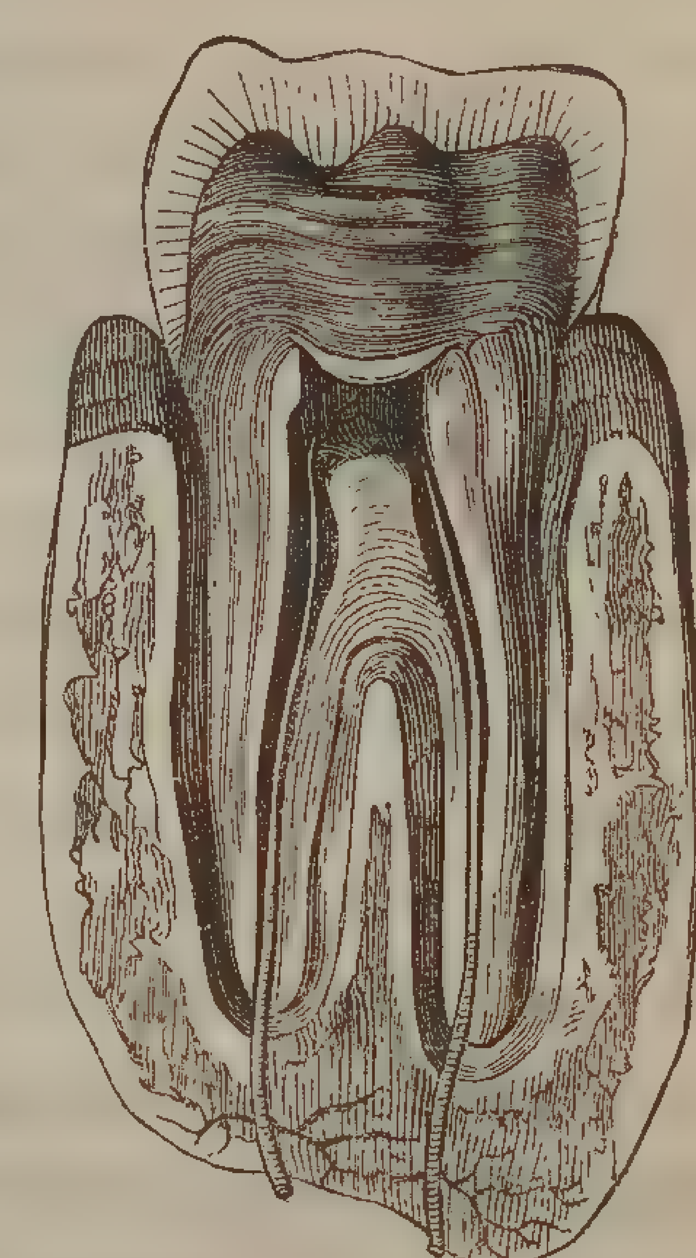
of the crown, and has the same external dimensions as the crown at a future period, has no organic connection with the matrix; it is formed by the deposition of the mineral components of the tooth mixed with some animal matter, and may be lifted off its matrix. Once formed, it is increased in thickness by the addition of layers of new matter to its inner surface by the pulp, which diminishes in size in proportion as the tooth increases in thickness. At the time that the tooth is cut, its growth takes place chiefly downwards into the jaw; a corresponding increase of the pulp downwards being of course simultaneous with the growth of the tooth. The inferior portion of the pulp takes the form of the future roots of the tooth, and continues to secrete more dental substance on its surface as it extends from above downwards; so that the roots of the tooth surround the radicles of the pulp in the form of hollow sheaths, which are at first short, but are gradually elongated together with the soft roots of the pulp by the continued apposition of new matter. The growth of the roots gives rise at the same time to the eruption of the teeth through the gums. At first the roots are merely thin sheaths with wide orifices, but they gradually become thicker by deposition on their inner surface, while the pulp becomes contracted; and at length they become pointed like the spines of animals, of which the root is the part last formed, and is likewise thinner than the middle portion of the spine. The roots of the teeth are at last nearly closed at their extremity, the only openings left being foramina for vessels and nerves passing to the remains of the pulp in the cavity of the crown of the tooth (see fig. 29).

The grinders of the ruminantia and horses, and the incisor teeth of the rodentia, are being constantly worn away at the crown, but continue to grow at their root for a long period during their life. As long as the crowns of the grinding teeth of ruminants are not worn, they have no roots; and, by the time that the roots are developed, the crown is already worn away. The tusks of the elephant, and the incisor teeth of the roden-

tia, always remain hollow at their root, and continue to grow by the successive deposition of new matter on the inner surface by the conical pulp which fills the cavity.

On feeding animals with madder, Hunter found that the substance of the tooth which was already formed never became coloured ; but that the innermost layer, which was just being deposited, became impregnated with the colouring matter.

Fig. 29.



The *enamel* of the tooth, which invests only the crown, consists of fibres which are placed almost perpendicularly to the surface of the tooth (fig. 29). During the formation of the tooth, this matter is deposited as a secretion on the surface of the crown, not by the pulp, but by the internal surface of the sac or follicle. The fibres forming it have almost a crystalline appearance.

Crusta petrosa.—In the ruminantia, horses, and several other animals in which the upper surface of the tooth is worn away, a new substance is added to their teeth after the crown has made its way through the gum ; this new substance is deposited on the sides and surface of the crown of the tooth, and fills up the inequalities of the crown, while the prominences formed by the other parts of the tooth are worn away by mastication. This new substance is the cement or crusta petrosa. It seems to be merely a deposit from the salts of the saliva, and to be essentially the same as what is called tartar on the human teeth. The perpendicular lamellæ of the elephant's teeth, which are each covered with enamel, are also ground away by the mastication of the food, and their interspaces are filled up with the cement or crusta petrosa. In the ruminantia and horse tribe the crusta petrosa is certainly formed from the salts of the saliva after the tooth has pierced the gum ; but Cuvier has shown that in the teeth of the young elephant the secretion of this cement-like substance has already commenced in the form of drops while the tooth is still enclosed in its socket, and that this secretion is probably performed by the inner surface of the dental sac after the formation of the enamel is completed. I have seen the appearance certainly, as described by Cuvier, on the teeth of the young elephant in the museum at Paris.

A circumstance which at first sight seems opposed to the idea of the growth of the teeth by the mere deposition of successive layers, is the fact of leaden bullets being frequently found in the tusks of elephants surrounded on all sides by the substance of the tusks. But, supposing that these balls had penetrated into that part of the tusk which was

just being formed, it is easy to understand how they would become enclosed in the substance of the tusk as new layers were deposited.

[The structure of the teeth has been recently investigated very minutely by Purkinje.*

The substance which constitutes the great mass of the tooth is formed of a homogeneous portion, and of fibres running parallel to each other from the external to the internal surface of the tooth. Purkinje believes that these fibres are really tubular; for, on bringing ink into contact with them, it was drawn into them as if by capillary attraction. This experiment was performed on the horse's tooth, and has been confirmed by Müller.† Müller has observed that the white colour of the tooth is chiefly owing to these tubes; when thin lamellæ of a tooth are examined with the microscope, the intervening substance is seen to be semi-transparent. The white colour and opacity of the tubes is removed by acids. In the more transparent portions of carious teeth, the white substance in these tubes had a granular and less compact appearance; and this appearance of a granular matter in their interior was also removed by acids.

From these observations, Professor Müller inferred that the tubes are filled, at least partially, with calcareous matter. On breaking a thin lamella of a tooth transversely with regard to the fibres, and examining the edge of the fracture, he perceived tubes projecting here and there from the surfaces; they were stiff, straight, and apparently not flexible. If the lamella had been previously acted on by acid, the projecting tubes were flexible and transparent, and often very long. Hence Professor Müller inferred that the tubes have an animal tissue; and that, besides containing calcareous matter in their interior, their tissue is in the natural state impregnated with calcareous salts. The greater part of the earthy matter of the tooth is, however, contained in the homogeneous transparent portion, in which it can be rendered visible in a granular state by boiling thin laminæ of teeth in a ley of potash.

Although the great mass of the tooth is destitute of organisation, there is a portion forming a layer both on the external and on the internal surface of the root; in which, by the aid of the microscope, Purkinje has discovered the corpuscules which characterise the structure of true bone. He has discovered the same bodies in the crusta petrosa of the teeth of several animals.]

The tooth-ache is seated in the pulp—the only sensitive part,—and the sensation excited in the teeth by the action of acids is likewise seated in this part; in the latter case, it is probable that the acids permeate the invisible pores of the tooth and act on the pulp itself. What is called

* [His observations were published in a dissertation by Fraenkel, De penit. Dent. Human. structurâ. Vratislav. An account of them is given in Müller's Archiv. for 1836. Jahresbericht, p. i.]

† [Archiv. 1836 Jahresb.]

caries of the teeth, is very different from the morbid process in bones known by that name. It is merely a chemical decomposition of the teeth, effected gradually by the fluids of the mouth; the teeth themselves being of abnormal composition.*

In their *chemical composition* the enamel and osseous substance of the teeth differ, the latter containing much more animal matter (cartilage). The following presents the result of the analysis of the two substances in man by Berzelius:

	Enamel.	*Osseous substance.*
Animal matter	——	20·0
Phosphate of lime with fluate of lime	88·5	64·3
Carbonate of lime	8·0	5·3
Phosphate of magnesia	1·5	1·0
Soda with some chloride of soda	——	1·4
Free alkali and animal matter	2·0	——
	100·0	100 ·0

The crusta petrosa of the teeth of the ox is found by Lassaigne to consist of animal matter 42·18, phosphate of lime 53·84, and carbonate of lime 3·98, in 100 parts.

Some physiologists, observing that teeth are formed by the deposition of successive layers, and that in birds, tortoises, and whales, as well as in the ornithorhynchus, they are replaced by bodies formed of horn, have been induced to class the teeth among the horny structures, and have supposed that the animal matter of the teeth is horn. This is quite erroneous. After the extraction of the calcareous matter, the teeth yield true gelatin on boiling,—this I know from my own observation,—while gelatin can never be obtained from horn by coction. The animal matter of horn, and that of the teeth, are therefore quite different substances; and the presence of gelatin in the teeth seems to be required to bind together the calcareous matter.

The teeth of the ornithorhynchus are connected by a broad base with the gum, and consist of hollow fibres of horn.† The teeth of the orycteropus also consist of perpendicular conglutinated tubes, to which, Cuvier says, blood-vessels are sent; but they are not horny. Those of the ornithorhynchus, however, consist, according to Lassaigne, of 99·5 parts of horny substance, and 0·3 parts of osseous matter; they thus evidently form the transition between the true teeth and the horny lamellæ by which their place is supplied in the whales.‡

* Interesting observations on the growth of the teeth of different animals will be found in Meckel's translation of Cuvier's Anatomie Comparée. Band iii.

† Heusinger, loc. cit. 197.

‡ The structure and mode of growth of the whalebone lamellæ have been investigated by Heusinger and Rosenthal, Abhandl. der Akademie zu Berlin, 1829; [and recently by Ravin. Ann. des Sc. Nat. 1836.]

3. *Of the texture of the crystalline lens.*—The crystalline lens of the eye consists of concentric lamellæ enclosed one within the other. It has been observed that these lamellæ or capsules are again formed of fibres by which the thickness of each is determined. The fibrous appearance is not due, Arnold remarks,* to the action of alcohol, hot water, or other similar reagents, for he has seen the fibres even in lamellæ of perfectly fresh lenses, though not distinctly; the fibrous structure is seen better after the lens has been immersed in dilute alcohol. Leeuwenhoeck, Huenefeld, Reil, and Arnold, describe the arrangement of the fibres in the laminæ to be as follows:—Let three lines be imagined extending from the centre of the anterior surface of the lens or its axis to the border, dividing the surface into three spaces. The fibres run parallel to each other from the border of the lens through the laminæ obliquely towards these three lines, so that each lamina consists of three fibrous compartments. The three lines form a figure free from fibres, which is bounded by the fibres of the three compartments of the laminæ. I may here remark that, in the eyes of most hogs, the division of the lens into three such compartments may be seen externally.

[The description which Sir D. Brewster gives of the arrangement of the fibres in the lens of most mammalia does not differ materially from the above: he finds, however, that in birds, fishes, some reptiles, and a few mammalia, their disposition is more simple. The fibres are united laterally to each other by a series of teeth; those of one fibre being received into hollows between the teeth of those in contact with it.]

Arnold calls the fibres lymphatic vessels; but they are really merely fibres. The fibrous structure of the lens may depend merely on the mode in which the substance of the lens is secreted, in the same way as the enamel on the teeth of the ruminantia, in the fœtus of which I have found the enamel, while still soft, to consist of almost parallel perpendicular fibres, which afterwards disappear or become cemented together by their interspaces being filled up.

The matrix of the crystalline lens is its capsule, which seems to secrete the layers of the crystalline from its inner surface. It is not, however, ascertained with certainty that this is the mode of its formation; it is not exactly known whether the lens has not some intimate organic connection with its capsule. Werneck† asserts that the inner surface of the capsule is connected with the lens by a tissue of very minute cells, which, when the capsule is very carefully torn from the lens under water, remain attached to its inner surface. The blood-vessels of the capsule have been already described at page 215.

The chemical composition of the lens has been examined by Berzelius. The matter composing it is nearly wholly soluble in water; it is coagu-

* Untersuchungen über das Auge des Menschen. Heidelb. 1832.

† Zeitschrift für Ophthalmol. iv. p. 28.

lated by heat, and the other agents which coagulate albumen and the colouring matter of the blood. The fluid which remains after its coagulation is slightly acid, and contains osmazome with its usual concomitant salts.

Albuminous matter	35·9
Alcoholic extract with salts	2·4
Watery extract with traces of salts . . .	1·3
Animal matter insoluble in water . . .	2·4
Water	58·0
	100·0

The ash left after calcination is said to contain iron. The alkali and chloride of sodium, with some phosphate of lime, amount together to $\frac{1}{200}$th of the weight of the fresh lens. A lens which had lost its transparency was found by John * to have an alkaline reaction.

Slight wounds of the capsule of the lens are said by Dietrich † to produce no manifest effect. Larger wounds of the capsule, with disturbance and wound of the lens itself, were followed by opacity of the lens to its very centre, from which it spread to the circumference. The occurrence of lenticular cataract, which frequently commences in the hard nucleus of the lens, does not prove that the lens itself is supplied with vessels; for a change in the secretion from the inner surface of the capsule might give rise to the production of a chemical change in the central laminæ of the lens, which it will be remembered are more dense than the external layers, and are perhaps of a different chemical composition.

The production of a cataract very probably depends on a change in the condition of the capsule. Inflammation of the capsule, though not the only cause of cataract, is stated by Professor Walther to be a very frequent one; and a preparation in the possession of Schroeder van der Kolk, in which the capsule of a cataractous lens is very beautifully injected, which is known to be done with great difficulty in adults, tends very strongly to confirm his opinion.

c. Of the laws of growth and changes of form.

The growth,—that is, the increase in size of organised bodies,‡—has a determinate limit, which in most of the higher animals is arrived at long before the end of life,—in man, for instance, at adult age; while the change of form which the whole body, or different organs, undergo, continues without cessation. In many plants, in fishes, and in several reptiles, the

* Meckel's Archiv. iii. 361.

† Ueber die Verwundungen des Linsensystems. Tüb. 1824.

‡ The laws which regulate the growth of organised bodies, have been treated of by G. R. Treviranus in his Biologie, vol. iii. 463—544, in a very instructive manner, and with his accustomed philosophic acuteness.

term of growth and that of life are nearly the same. But all parts do not grow uniformly; and many disappear, while others are formed and become developed: growth is, in short, accompanied by constant changes of form. In the majority of animals the most remarkable phenomena of change of form occur during the period of fœtal life; this is the case in man, mammalia, birds, and fishes; while in the amphibia, insects, and several of the lower crustacea, the embryo state seems to be prolonged for a considerable time after the developement of the ovum is complete, their external form undergoing change, new organs being formed and others lost. The changes of form, after birth, are most rare in man and mammalia: instances of them are however afforded by the growth of the thymus gland at the commencement of childhood, and its subsequent wasting up to the twelfth year; by the period of developement in which the change of the teeth takes place; and by that of puberty, during which the larynx changes its form, and the breasts, and the bulbs of the hair covering the chin and pubes, are developed. But in *amphibia* the changes of this kind are much more extended. Even the kidneys are not developed until the animal has acquired the condition of the tadpole, when the corpora Wolffiana, described at page 153, waste away. The disappearance of the external branchiæ in the tadpole, the developement of the internal branchiæ which continue to exist during the greater part of the larva state, the disappearance of the tail, and the final loss of the branchiæ, have been already mentioned. The generative organs are not developed till near the termination of the larva condition. I could not discover any trace of the testes and ovaries before the transformation into the perfect state had commenced, when the animal had already four extremities, although it still retained the tail and branchiæ. Even in the salamanders, which have extremities during the greater part of their larva state, the genitals are not developed till near the termination of this condition, just before the branchiæ are lost. The intestinal canal of the frog in the larva state was destined for vegetable food, and was consequently of extraordinary developement; during the metamorphosis it is reduced to the condition of the canal in carnivorous animals. The vertebræ, also, which in the larva state were connected by excavated facets, as in fishes, undergo change at the same period.

The metamorphosis which animals undergo during the processes of developement and growth depend partly on the developement and reduction of similar parts.

It has been said that the embryo, during its developement, passes through stages of developement which are permanent conditions of lower animals; and this idea, incorrect in itself, has been extended to an extravagant length. But in the hypothesis may be perceived some presentiment of the real law, which however escaped the observation of those who opposed it. Von Baer has the merit of having first discovered the real

relation which the phenomena bear to each other; he pointed out, that in the vertebrata, from man down to fishes, there is one common type of formation, a certain sum of similar organs, which in the embryo state of all are met with in perfect similarity, but which during their developement assume different forms in different classes of animals, or are even reduced to a state lower than the original type; thus, for instance, in the embryo state of all the vertebrata the os hyoides has rib-like appendages, but in the higher classes these are partly lost, while in fishes, and the larvæ of the amphibia, they are developed to form the branchiæ.*

All the *vertebrata* resemble each other in presenting a series of vertebrate bones with arches posteriorly to protect the central parts of the nervous system, and a number of anterior appendages in the form of ribs to enclose the viscera. A part of these anterior appendages meet cartilaginous or osseous ribs connected with the sternum, thus forming a thorax; while the ribs belonging to the cervical and lumbar vertebræ are absent in many of the vertebrata, and in some (the crocodilida and lacertæ) the appendages of the cervical vertebræ are merely rudimentary. In all the vertebrata, the vertebral system here indicated dwindles away to an imperfect condition inferiorly under the form of the coccygeal vertebræ, and is more highly developed superiorly in the three vertebræ of the cranium. More than three vertebræ I cannot discover in the cranium; to mark out vertebræ in the ear, &c. seems to me to be an exaggeration and an abuse of an analogy which is to a certain extent quite correct. In all embryos of the vertebrata the extremities are at first absent; their first form in all is that of small prominences, which afterwards take different forms in the different classes. Thus we see how the forms of the developed vertebrate animals depend on the transformations and reductions of one common type. Some animals during growth deviate more, others less from the form which this type presents in the embryo and larva state.

In the *articulate classes*, in which the brain, it is true, lies above the œsophagus, but in which the nervous cord, that forms its continuation through the intervention of a ring which surrounds the œsophagus, runs along the abdominal surface of the body, a common type peculiar to them is again evident, consisting of a series of rings enclosing the body, and connected with each other in a series from before backwards. The maxillæ and mandibles appear, from Savigny's researches, to belong to one and the same system of organs with the feet.

The *insect*, while in the larva or caterpillar condition, has thirteen rings or segments of the body; it is only during this state that it increases in size, changing its skin three or four times: by the metamorphosis which it undergoes during the pupa or chrysalis condition, it is converted into

* See page 301.—The note.

a new creature. Before the organising power which produces this change of form can be exerted, it is necessary that the uniform members of the larva shall have attained a certain size. The continued nutrition of the parts of the larva by the introduction of food, seems to delay the production of the metamorphosis, for the insects undergo transformation earlier when no food is given them, just as plants blossom earlier in poor soil; but in proportion as the parts of the larva, as yet uniform, increase in size, the stronger seems to become the tendency to the production of differences of form in them, by the reduction of some parts and the developement of others.

When the last change of the skin takes place, the insect, enveloped in its cocoon, assumes the chrysalis form; the external tegument of which, like all horny matter, is at first soft. In the external form of many pupæ the rudiments of the exterior figure of the future insect may be already traced, the extremities being pressed close to the body. The fundamental features of the change in the external form of the insect are displayed in the transformation of the larva to the pupa. The division of the future animal into three parts is already seen; the three rings of the body which follow the first, or cephalic ring, being converted into the thorax, in which the protothorax, mesothorax, and metathorax are afterwards recognised, while the posterior nine of the thirteen segments become shortened, and form the nine rings of the abdomen of the perfect insect; the rudiments of the wings are formed on the second and third ring of the thorax; the antennæ and palpi on the head or cephalic ring. The organs for the perception of light do not exist in many insects until they undergo transformation; in others compound eyes are then developed in the place of the simple eyes of the larva. Of the thirteen ganglia of the nervous cord in the larva of the cabbage moth,—papilio brassicæ,—the third becomes united with the fourth, and the fifth with the sixth, while the seventh and eighth wholly disappear. The viscera undergo corresponding changes. The butterfly acquires a proboscis in place of the maxillæ of the caterpillar; its vessels for the secretion of the web disappear. The intestinal canal and respiratory organs are changed in form. From the commencement of the metamorphosis the fatty body is rendered almost fluid; it is chiefly employed in the formation of new organs. While in the larva of amphibia the generative organs are at first absent, Herold has found, in insects, extremely delicate rudiments of the testes and ovaries, even in very young larvæ. Many insects retain the larva type.*

With regard to the *crustacea,* it is observed, not only that the higher species in their embryo state have a thorax composed of distinct segments, and thus resemble the permanent condition of the lower

* For further information on the metamorphoses of insects, consult the classical work of Herold, Entwickelungsgeschichte der Schmetterlinge. Cassel, 1815.

species, but that the young crustacea are also often much more simple than afterwards,—for example, the young cyclops has but two antennæ and two pairs of feet. Some crustacea indeed undergo a perfect metamorphosis; this is the case with the lernæa tribe. The proper place in the scale of animals for these strange parasitic creatures was long doubtful, because when fully formed they had lost almost all traces of their former division into segments; hence many classed them improperly with the entozoa. Nordmann* has discovered that in the embryo and larva states these animals have the form of perfect crustacea. The embryo of the achteres percarum has, for instance, four pencil-like feet. After it has left the ovum, it has two antennæ, three pairs of anterior cheliform feet, and two pairs of flabelliform feet, and is similar to the fishlouse (caligus). The young of the ancorella, even while in the ovum, have a red eye.

During the growth of the *annelida* the number of their rings increases, and in the arenicola the number of the tufted branchiæ also; at least I am induced to think so on comparing different specimens of the arenicola carbonaria.

CHAPTER III.

OF REPRODUCTION.

The continued operation in the process of nutrition of the same creative principle which in the embryo models all the individual parts of the animal, as members as it were, all necessary to constitute the whole, enables the system within certain limits to recover from the exhaustion that follows action and from injury, and to reproduce parts that are lost.

Laws of reproduction.—The power of reproduction is greater the more simple the structure of the animal, and in the more complex animals proportionally with their youth. Thus the larvæ of the amphibia, in which many parts are first formed which in other animals are developed in the embryo state, have also a greater power of reproducing lost parts of the body than the perfect animal; in the larvæ of insects also lost parts are often regenerated; in the perfect insect this is never the case. In the case of the lower animals, such as polypifera and worms, a mere fragment separated from an individual will reproduce a perfect animal. The gradual diminution of the reproductive power in proportion as an animal is more complex in its structure, or is more advanced in its developement, cannot be accounted for otherwise than by supposing that, by the developement of the body, the formative principle becomes, as it were, more divided, and in part fixed in the separate organs that it has itself created.

In the Prolegomena I have already mentioned some of the general

* Microgr. Beiträge. ii.

laws by which reproduction is regulated. When, as in very simple animals and plants, a perfect individual consists of a certain sum of similar parts, and grows simply by increase of the number of these similar parts, the perfect being may be divided, and the separate portions will still contain the essential parts of the integral being, though in smaller number, and each portion will continue to live and form itself into a perfect being. Thus it is that cuttings of plants placed in the ground grow and become new productive individuals. The different parts of a plant are essentially so similar to each other, that branches can transform themselves into roots, and stamens into petals. In the same way the regeneration of the fresh-water polypes,—the hydra, and similar animals,—may be explained; although the polypes, judging from the structure of the infusoria, are certainly much more complex in their organisation than was formerly believed.

The arms of the hydra separate spontaneously from the rest of the animal, and develope themselves to new individuals;* we cannot, therefore, be surprised at their becoming thus developed when cut off. But, even if polypes are divided either transversely or longitudinally, each half will become a perfect animal; small portions indeed cut from one of these creatures will become so many perfect polypes. If now we imagine a polype to consist of a system of particles which have similar vital properties, and which are subjected to the formative principle of the individual only so long as they have a certain affinity for each other, and if we suppose the formative principle to be the result of the mutual action of the molecules, pieces cut from such a polype will also contain systems of such molecules. The organising principle resulting from the affinity of the particles for each other, will be in operation in them also, and will impart to each fragment the organisation of a new individual. When the polype has attained a certain size, and the system of homogeneous particles has become large, there seems to arise in small portions of the animal an affinity of the molecules forming each of these parts, for one another, greater than that of the different parts of the whole for each other, and thus is produced a tendency to the formation of gemmules which separate from the parent animal and become independent polypes. For the same reason, also, fragments partially separated from a polype become individualised and separate from the parent body as new individuals. Goeze, Schaeffer,† and Roesel‡ assert that polypes may even be completely everted and still continue to grow. If now these facts are applied to the germ of the higher animals, it will appear that the only period during which it can be capable of division and reproduction, is while it consists of a

* Trembley, Histoire d'un Genre de Polypes d'Eau douce. Leide, 1744. Translated into German by Goeze. Quedlinb. 1791.

† Abhandl. von den Armpolypen.

‡ Insectenbelust. iii.

homogeneous substance, in all parts of which the formative principle by which the individual organsiation is to be effected is equally distributed. If we imagine the germ of any animal high in the scale to be from some unknown cause cleft for a certain distance, either at the part where the head, or at that where the tail is at a later period formed, or, without any cleft being formed, the parts to be developed doubly in the direction of the axis, the consequence must be, if the laws above laid down are correct, that two heads or two caudal extremities, and thus a twin monster, will be formed, just as in the case of a planaria partially divided artificially into two portions.* All the cases of twin monsters are not explicable by this division of one germ, nor all by the growing together of two germs. The concretion of two germs, or the production in one germinal membrane of two embryos which have afterwards grown together, affords the best explanation of a great part of the double monsters, particularly where the double portions are large. The fact of the growing together of two embryos is proved beyond doubt by the cases in which the embryos are united by but a small portion of the body,—for example, by the occiput, as in Barkow's† case. Embryos of animals, which are united by the face, and are single only in the snout, but elsewhere double,—or double monsters, of which the head is single and the whole trunk double,—cannot be well explained by the supposition of the germ having become cleft; they are produced by the union and fusion, as it were, of the germs together at some point where similar parts would in each be at a later period found; the snout of the one, for example, unites with the snout of the other; the corresponding parts seeming in this case to exercise a certain attraction one on the other. On the other hand, it would be equally difficult to account for the formation of a monster with a supernumerary part, such as a supernumerary finger, or of a perfectly single body with a double snout, on the supposition of the union of two germs. The laws admitted to exist in the reproduction of polypes must without doubt be equally valid also in the case of the simple germs of the higher animals. There are but two instances on record of double monsters of the common fowl having been obtained for examination before the disappearance of the germinal membrane. The one is described by C. F. Wolff;‡ the other by V. Baer.§ In Wolff's case both the embryos were perfect, and were connected only by that portion of the germinal membrane which is continuous with the intestinal canal at the umbilicus. In Baer's case the area pellucida, instead of its usual circular figure, had more a crucial form. The embryos had but one head in common, and their bodies diverged from it in the

* J. Müller, Meck. Arch. 1828, 1.

† De Monstr. dupl. vertic. inter se junctis. Berol. 1821.

‡ Nov. Comment. Acad. Petrop. xiv. 456. § Meckel's Arch. 1827, 576.

longer branches of the cross. We shall, however, return to this subject in the eighth book, which treats of the history of the developement of organised beings.

Dugès* has shown that the *planariæ* have a great degree of reproductive power. The animal being cut into eight or ten parts, each part is able to reproduce a perfect individual. The reproduction was completed in winter in twelve or fourteen days, in summer in four days. Sometimes the planaria divides spontaneously into two individuals by transverse division of the body. Dugès found in some water a planaria of which the posterior part of the body was double, and by dividing one longitudinally at the anterior part of the body a double monster with two perfect heads was produced.

In the *annelides,* the vascular trunks, the gangliated nervous cord, and the intestinal canal extend the whole length of the animal through the annular segments of the body in a tolerably uniform manner. This structure of the animal—its consisting of a series of parts, of which each contains similar organs,—explains the circumstance that, although so complex in its organisation, division of its body transversely does not prevent the reproduction of the worm. O. Fr. Mueller† observed reproduction take place in portions of divided nereides; and Bonnet‡ saw each portion of a nais variegata, which had been divided into four, five, or six parts, reproduce a perfect animal, and each half of an earthworm which he had divided transversely was regenerated to form a perfect worm. Dugès did not obtain the same result from the latter experiment; but he found that, when the head and anterior rings of the earth-worm were cut off, they were reproduced.§ When any of these animals are divided longitudinally, the halves are not regenerated, probably because the essential elements of the individual are no longer contained in each portion.|| The naides divide spontaneously.¶ Leeches, according to Moquin Tandon, possess little or no reproductive power.

The *mollusca, insecta, crustacea, and arachnida* have only the power of reproducing single parts; and it is certain that the reproduction of a part of the head with the antennæ in snails does not take place if the brain, which lies above the œsophagus, is injured by the wound; it requires, moreover, a moderate temperature, and is not effected when the temperature is very low.** Heineken†† states that arachnida

* Froriep's Not. 501. Annal. des Sc. nat. 1828.

† Von den Würmern des Süssen und Salzigen Wassers.

‡ Contempl. de la Nature. § Froriep's Not. 513.

|| The earlier observations relating to this subject will be found in the great works,—Treviranus, Biologie, and Burdach's Physiology,—and in a small treatise of Eggers, von der Wiedererzeugung. Würzb. 1821.

¶ O. F. Müller and Dugès, loc. cit. and Gruithuisen, Nov. Act. Nat. cur. t. xi. tab. 35.

** Schweigger, Naturgesch. der skeletlos. ungegliederten Thiere.

†† Froriep's Not. 606, 607.

lose the power of reproducing their legs after they have ceased to change their skin, or are fully developed. The larvæ of insects reproduce their antennæ when lost, the perfect insects do not. The phasmæ in their imperfect larva condition reproduce their legs if lost. The regeneration of the claws of crustaceous animals is a well-known fact.

In *fishes* the only known instance of reproduction is that of the fins, mentioned by Broussonet. In the class of *reptiles* the phenomenon of the reproduction of lost parts is presented by lizards, in which the tail when lost is restored; but the new tail contains no perfect vertebræ, there is merely a cartilaginous column in their place.

Spallanzani* has observed reproduction of the tail in the *salamander* likewise. We have here an example of the reproduction of the posterior part of the spinal cord. Experiments have been instituted on the reproductive power of salamanders by Spallanzani, Bonnet, Blumenbach,† Steinbuch,‡ and Rudolphi. In salamanders, young as well as old, the legs are reproduced; and Rudolphi has observed that in the new limb no line can be perceived in the nerve, marking the point at which the new nerve commences. In the salamander the under jaw is also reproduced; and in the triton Blumenbach has seen even the eye, with cornea, iris, and lens, reproduced within the space of a year. For the reproduction of the eye it is necessary, however, that the optic nerve and a portion of the coats of the eye should remain uninjured at the bottom of the orbit. The blastema, from which in these cases the individual parts of the lost organ are formed, is at first gelatiniform and transparent: on the stump of the excised leg or branchia of the larva of the triton it has the form of a globular mass of gelatinous substance, which, according to Steinbuch, is at first not vascular; it is seen as early as the second or third day on the stump of the branchia. The mass increases, and assumes the form of a cylinder; but in a few days it becomes organised and traversed by blood.§ In an experiment which I performed myself, this took place much less quickly. Dieffenbach has observed that after a wound of the skin, muscles, and periosteum in the salamander, the whole limb, whether extremity or tail, often separates, and is afterwards reproduced.

We have already discussed the question respecting the particular power to which the reproduction of parts so complex in their organisation in adult animals is to be attributed,—whether to that formative power to which even the nerves are subject, and by which the nerves are originally formed, or to the influence of the nerves themselves. If the latter view of the question were adopted, it would be an interesting fact, that the remaining trunk of the nerve contains all the fibrils

* Physic. Mathem. Abhandl.

† Spec. physiol. comp. inter animantia calidi et frigidi sanguinis. ‡ Analecten.

§ See page 375.

the continuations of which had been distributed in the textures of the lost limb; the nervous stems generally being only the aggregate of the primitive fibres which are distributed in the branches and twigs. A division of the nerve at a second place above the stump is said* to prevent reproduction of the limb.†(?)

It is probable, however, that the reproduction even of the nerves is dependent on a higher power, since in the metamorphoses which animals undergo the nerves suffer a change of form as well as the other parts.

All the phenomena of reproduction hitherto considered take place without the occurrence of inflammation; they consist in the formation of a blastema and its organisation, just as in the first developement of organs. In the lower animals the phenomena of inflammation, if they occur at all, merely precede those of reproduction, as the immediate effects of the wound. In frogs suppuration is indeed observed in some cases; I have myself seen it. In snakes I found that the wounds became quickly covered with a crust. In the higher animals, complex organs, such as the extremities or eyes, are never reproduced; single tissues merely are regenerated.

Regeneration of tissues.

Regeneration of the different tissues is observed under two forms; in one unaccompanied by inflammatory action, in the other combined with inflammation.

1. *Regeneration unaccompanied by inflammation.*

a. Organised tissues which, having lost their organisation, are reproduced.—Of these we have examples in the shell of the crustacea, the antlers of the deer, and the organised bulbs of the feathers and spines.

The shell of the crab is renewed every year when the developement of the internal organs renders the size of the old shell inadequate. The shell becomes cleft, and is thrown off in August, disclosing a new one already formed beneath it; which, however, is at first soft and endued with sensibility, and even contains vessels, although it soon becomes hardened by the deposition of carbonate of lime in it.‡ At the time of the change of the shell, chalky concretions—lapides cancrorum—are formed on each side of the stomach, and disappear as soon as the new shell is hardened. The stomach of the crab is said to renew its epithelium.

The *antlers of the deer*, and similar animals, have more analogy with the organised matrix of the horns of ruminating animals than with the

* Todd, Quarterly Journ. of Sciences, vol. xvi. p. 91. Treviranus, Erschein. und Gezetze, ii. 7.

† [See the account of Dr. Sharpey's experiment, page 374.]

‡ Cuvier, Anat. Comparée.

horns themselves. The base of the antler rests on the tubercle of the frontal bone, a bony jagged enlargement marks the point of junction of the antler and this tubercle. The males throw off the antler, not at the rutting season (autumn), but in the spring, and new antlers are then developed. The separation of the old antler is effected by a kind of softening of the organised bony substance of the tubercle of the frontal bone at the point of its junction with the antler; the rough surface of the tubercle, that is left, is soon covered again by skin. The new antler begins to rise from the frontal process, covered by skin and periosteum; it is at first soft and cartilaginous, and traversed by innumerable vessels. While the cartilaginous mass becomes ossified,—presenting a repetition of the process which takes place in the fœtus and young animal,—the periosteum and cutaneous covering of the antler lose their vitality and drop off; after castration young stags acquire no antlers, and those of old stags are not changed.*

In the same way the organised *bulbs of the hair and spines* in mammalia, *and of feathers* in birds, have their alternate periods of wasting and turgescence; and hence the casting of the coat of mammalia, and the moulting of birds, during which the hairs and feathers fall off and new ones are produced. The reproduction of hairs and feathers, however, so far differs from that of antlers, that in the hair it is merely the matrix, and in the feathers the bulb, which resemble the organised antlers, and the shrunken and dry remains of the bulb in the quill resemble the hardened antlers which have lost their vitality. The horny substance of the hairs and feathers is secreted by the matrix, and the only part in the antler analogous to it is the cuticle of the recent antler. The reproduction of these parts must therefore be considered apart from that of the antlers.

b. Unorganised textures which are reproduced by the regeneration of their matrix; such are the horny structures, the teeth, and the crystalline lens.

1. *The horny structures.*—The nails, it is well known, are reproduced if their matrix is not destroyed; but the commencing formation of a nail has been observed, even on the middle phalanx of an amputated finger.†

The shedding of the coats of mammiferous animals has been investigated by Heusinger.‡ He plucked out a whisker hair of a dog, and found, five days afterwards, that a new hair, more than two millimeters in length, had been formed. During the casting of the coat the bulbs of the old hair become pale, and by the side of each a small black globular body is formed, which is developed into the new hair. This is a

* Ibid. Berthold, Beiträge zur Anat. Zool. u Physiol.

† Blumenbach, Instit. Physiol. p. 511. Dr. Elliotson's Physiology, p. 249.

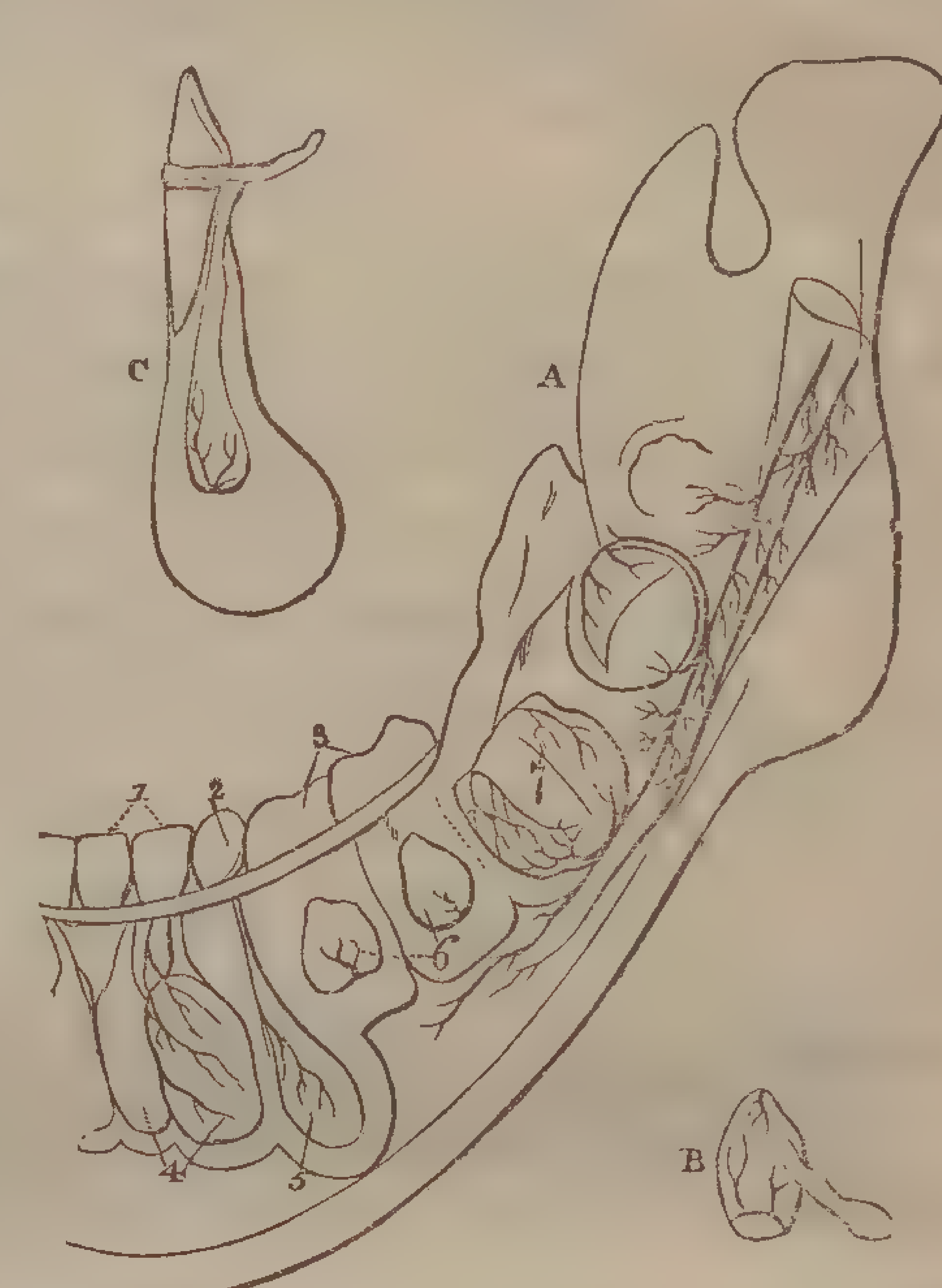
‡ Meckel's Archiv. 538.

very interesting fact; the matrix of the new hair is not the old pulp, but is, as it were, a new sprout from the productive base of the follicle. The spines (of the hedgehog, &c.) are said to be reproduced in the same mode. During moulting, the cuticle on the bill of birds and other parts is cast off in form of plates or of branny particles. The bulb of the new feather is already formed before the old feather falls out.*

Several writers† assert, as the result of experiment, that hairs plucked from their follicles, and inserted into punctures of the skin, will take root and grow. This statement appears to me, however, to require further confirmation. The interior of the bulb of the hair being organised, a union of it with other parts of the skin besides the fundus of the hair follicle, may certainly be supposed to be possible; but how easily may the experimenter be deceived in this observation! I do not know whether my much honoured friend Dieffenbach, who has been so successful in his observation on the reunion of divided parts, still attributes any value to this experiment, which he made in his youth.

2. *The teeth.*—The crown of the tooth being unorganised, and consequently incapable of growth, so as to correspond with the increased size of the jaw-bones, the formation of new teeth becomes necessary. The permanent teeth begin to appear about the sixth or seventh year, but their crowns are formed at a very early period. Of the twenty temporary or milk-teeth, eight only are molares; the permanent teeth are thirty-two in number, and of these twenty are molares, or twelve true molares, and eight bicuspides.

Fig. 30.‡



The situation of the permanent teeth with regard to the milk-teeth is peculiar [see fig. 30, A]. The three molares of the second set lie

* See A. Meckel, Reil's Archiv. 12. Eble, loc. cit. Burdach, Physiol. Bd. iii. 524.

† Dzondi, Beiträge zur Vervolkom. der Heilkunde. Halle, 1816. Dieffenbach, De regenerat. et transplant. Herbip. 1822. Wiesemann, De coalitu partium à reliquo corpore prorsus disjunct. Lips. 1824.

‡ [Growth of the permanent teeth, after Blake.—A. Relative position of the milk-teeth, and those of the second set. 1. The incisor teeth; 2. the canine tooth; 3. the molares of the first set; 4. the sacs of the incisor teeth; 4. that of the canine tooth; and 6, the sacs of the bicuspides of the second set; 7. the first permanent molaris, situated together with the second and third in a line with the teeth of the first set. B. The mode of connection of the cysts of an incisor of the first and second set; C. the same at a later period.]

in a line with the milk-teeth, being formed external to the posterior molar of the first set; they agree also in the form of their crown with the molares of the first set. On the other hand, the bicuspides, which do not correspond to the temporary molares in form, together with the canine and incisor of the second set, lie originally behind the molar, canine, and incisor teeth of the temporary set. The sac of the first great molar of the permanent teeth is developed as early as the end of the fourth month of pregnancy, the sacs of the permanent incisors at the end of the eighth month of pregnancy, then the sac of the canine tooth, and afterwards the sac of the penultimate molaris; the follicles of the bicuspidati are not formed until some months after birth, and that of the last molaris not till the fourth year.* Blake and Meckel both describe the cysts of the permanent teeth to be processes of those of the milk-teeth [see B, fig. 30]. But Meckel says that it is the outer membranes only of the follicles that are connected, while the internal membrane of the new follicle is developed by the side of that of the old cyst, between it and the external membrane.† The osseous matter of the first great molaris of the second set begins to be deposited towards the end of pregnancy. The sockets of the new teeth are gradually separated from those of the old [C. fig. 30], but the two cavities always communicate by a considerable opening through which the common portion of the external layers of the sacs passes. The change of the teeth commences about the sixth or seventh year. The first great molaris is the first of the second set which appears; then follow the incisors and canine teeth, the penultimate molaris not till the thirteenth or fourteenth year, the last molar between the sixteenth and twentieth year. The roots of the milk-teeth are absorbed before they fall out.

It has been frequently asserted that if the teeth of an animal, after being drawn, are re-inserted into their sockets, they will again take firm root. I doubt this very much. If a real organic union takes place in these experiments, it must be by the lacerated vessels of the pulp of the tooth uniting again with the vessels at the bottom of the socket. It is an interesting point which has not been determined so exactly as it ought to be. A sure way of deciding the question would be to feed animals, in which the teeth had been recently transplanted, with madder. If any vascular connection had been formed, the innermost layer of the tooth towards the pulp would be coloured red. The teeth not being organised, fissures in them, of course, cannot be closed by the reproduction of new dental substance; the fissures can, at most, be filled with crusta petrosa, or tartar from the salts of the saliva. In serpents new poison-fangs are being constantly reproduced. The new teeth of the crocodile press for-

* Meckel, Handbuch der Anatomie, Bd. iv.

† Meckel, loc. cit. p. 227; and in Meckel's Archiv. iii. 556.

wards into the conical cavities of the old teeth, the posterior wall of which becomes absorbed.

3. *The crystalline lens.*—It would appear that, in certain cases where the lens has been removed, it is reproduced by the capsule—its matrix. Leroy d'Etiole has observed this.* In the first case, thirteen days had elapsed since the extraction of the lens when the eye was examined; in the second case, thirty-three days; in the third, thirty-nine days; in the fourth, thirty-one days; in the fifth, forty-six days; and in the sixth, one hundred and sixty-five days. The experiments were made on rabbits, cats, and dogs. The contents of the capsule were either a crumbly mass, as in the second case; or a small lenticular body, as in most of the other cases; but in the sixth case a full-sized lens was found.†

2. *Regeneration accompanied by inflammation.*

Almost all cases of the regeneration of parts of the human body which retain their organisation, are of this kind, if we except the bulbs of the hair and teeth, which are reproduced, and even occur as morbid products in the ovaries and other parts. In the latter cases the hairs and teeth are formed in the same way as in their natural situation: the teeth have their covering of enamel, and are formed in follicles.‡

a. Regeneration which is accompanied by inflammation attended with exudation of lymph.

If the part, the subject of inflammation, has a free surface, whether there be a wound or not, an exudation of a coagulable fluid, the liquor sanguinis, takes place. If it has no free surface, the coagulable matter accumulates in the capillaries and in the texture of the part, and produces thickening and hardening. The matter effused in wounds, and on free surfaces of inflamed parts, is at first fluid; its first appearance on the surface of inflamed membranes being in the form of drops: it is then transparent, but gradually becomes milky and consistent. It is the fibrin which was in a state of solution in the blood. While the exuded matter is still in the fluid state, an impulse towards organisation seems to arise in it, by virtue of a vital property of the fibrin; and by the affinity and reciprocal action of the effused matter with the inflamed surface, organisation ensues. New vessels are formed in the exuded matter, probably in the mode suggested at page 376; the canals formed in the fibrin being first filled with fresh liquor sanguinis, and afterwards receiving red particles likewise. The idea of the prolongation of the free ends of vessels cannot

* Magendie's Journ. de Physiol. 1827, 30.

† See Mayer, Graefe in Walther's Journ. xvii. 1. Vrolik, ibid. xviii. 4. W. Soemmering, Beobachtungen über die organ. Veränderungen im Auge, nach Staaroperationen. Frankfurt, 1828.

‡ Meckel, Archiv. i. 519.

be entertained, since, indeed, no such free ends of vessels exist. The formation of new vessels in wounds, and in the liquor sanguinis which unites their borders, must be supposed to take place in the same way. A prolongation of the divided vessels cannot be well imagined. Besides, all the divided vessels are closed by coagulum. The organisation of the pseudo-membranes produced by exudation is not universal; those effused on mucous membranes,—for example, in croup,—generally do not, those on serous membranes usually do become organised. The organisation of effused lymph in very many cases cannot be doubted by any one who has once seen the beautiful injected preparations in Schroeder van der Kolk's museum at Utrecht, in which the arteries and veins of false membranes on different parts of the liver and intestines, and of those between the pleura costalis and pulmonalis, are seen injected with different coloured matters. Lymphatics, too, are formed in the new membranes, as several of Schroeder's preparations show; in which, by the sides of arteries and veins, I saw lymphatics filled with mercury. Schroeder says, "In hepatide verò chronicâ hepate pseudomembranis diaphragmati accreto, mihi contigit mercurium in vasa lymphatica impulsum in ipsas pseudomembranas propellere, ita ut vasa lymphatica nova in conspectum venirent; in his valvulæ vel noduli jam conspici poterant, licet minores quàm in aliis vasis lymphaticis; cum arteriis et venis cursum magis rectum servabant, aliquando tamen paulatim convolutum, aliquando quædam vasa lymphatica ad pseudomembranæ originem sursum tollebantur, sed postquam in pseudomembranam transire inceperant, arcu facto ad hepatis superficiem redibant; in illo arcu plura vasa lymphatica ex hepate terminabantur. An arcus talis prima vasorum lymphaticorum novorum origo?"*

The formation of new vessels between the portions of an arterial trunk above and below a ligature, or the point where it has been divided, is remarkable. It has been observed, and very similarly described, by Maunois, Parry, and Mayer. The fact cannot be doubted, particularly since Ebel's repeated experiments and his excellent drawings were published.† The new communication is effected by means of several vessels passing, sometimes in a serpentine course, between the two portions of the divided vessel—of the common carotid, for instance. In explaining this phenomenon the fact has been overlooked, that in other animals than man the common carotid gives off several very small twigs to the muscles of the neck, so that the vessels supposed to be newly formed are probably merely enlarged capillaries.

All organised parts will reunite, when divided, if the surfaces are brought in contact while they are in the state of adhesive inflammation; the divided ends of nerves will unite with nerves, or even with muscle,

* Schroeder, Observ. Anat. Path. 43.

† Ebel, De Naturâ medicatrice, sicubi arteriæ vulneratæ et ligatæ fuerint. Giessen, 1826.

periosteum, or aponeuroses; and parts even, which have been quite separated from the body, will unite when accurately applied to the surface of fresh wounds, whether of parts of similar or of different structure; but the inflammation in those parts must not exceed the stage of the effusion of lymph. This reunion of organised parts which have been completely separated from the body is certainly extremely rare, but its occurrence cannot be doubted. Buenger's remarkable case of the formation of a new nose from a piece of skin taken from the thigh is an instance of it.* All the cases, however, supposed to be instances of this phenomenon are not equally satisfactory. We can scarcely believe that in Hunter's case of the transplanting of a tooth of a dog into the comb of a cock, a real vascular union took place. In another experiment Hunter transplanted a gland taken from the abdomen of a cock to a similar situation of a hen; he also transplanted the spur of a cock; in both cases the removed part is said to have united in its new situation. Abernethy† has described these and other cases; Baronio has made similar experiments.‡ Merrem, and my illustrious teacher V. Walther, assert that the portion of the bone removed by the trephine will reunite.

The reunion of portions of skin only partly separated from the body with other parts is known to be effected very readily,—for instance, in the case of the formation of a new nose from the skin of the forehead, and in other surgical operations in which Dieffenbach has become so celebrated. When the skin has united in its new situation, the narrow portion by which it was left connected with the body may be divided. The union of two parts in which inflammation has been excited, is a very general phenomenon in organised bodies, and is taken advantage of in surgery for the removal of solutions of continuity, and as a means of putting stop to certain secretions. By this process the fœtus may become united with the membranes of the ovum, or two fœtus may become united together. A very remarkable law prevails in the union of embryos. Almost without exception, it is the corresponding parts of the two embryos that become not simply attached to each other but as it were fused together; the symmetrical parts of the one embryo, indeed, separate from each other at the point of union, and unite with the corresponding parts of the other embryo; thus are formed the monsters of Janus. Without the supposition that some kind of affinity or attraction is exerted between corresponding parts, unions of this kind are inexplicable. The union must in these cases, however, take place at a very early period; for when embryos become united at a later stage of developement, the parts of the two have merely a superficial connection.

* Froriep's Not. iv. 225. † Physiological Lectures, 253.

‡ See what I have said on the transplantation of teeth and hairs at page 408.

Rathke* has observed a case in which the umbilical cord of one embryo was united with the head of the other.

Regeneration of the different tissues.—The divided surfaces of a tissue generally unite when brought in contact in the state of adhesive inflammation; but the newly formed substance which unites them, and which is in all cases at first fibrin, does not, in the case of the tissues destined for sensation and motion, present in a perfect degree their peculiar properties. In most other tissues the regeneration is complete,—the new substance has the organic properties of the original tissue, particularly if it be one of those tissues which are less important from their vital properties than from the physical properties with which they are endued, which is the case with the bones. But tissues of this kind are not all reproduced with equal facility. The tendons, ligaments, and cartilages generally are regenerated extremely tardily; bones, on the contrary, very readily.

Brodie says, that, when ulcerations of the *cartilages* are healed, it is not by reproduction of the natural structure. Beclard states, that, in the case of a broken costal cartilage, the two surfaces become united by a plate of cellular substance, and external to this a bony ring surrounds the two ends of the cartilage. Dörner cut a small quadrangular piece from the thyroid cartilage of a cat, and at the end of twenty-eight days the opening was closed by strong membrane merely. Dörner found likewise that, when cartilages are divided by a single incision, direct union of the substance does not take place; the union of the divided perichondrium forms afterwards the only medium of connection.† The substance which reunites divided tendons has not, it seems, the fibrous shining aspect of tendons, but is more cartilaginous. According to Arnemann, the dura mater is never regenerated. (?)‡

The process of reproduction is most remarkable in *bone*. The more spongy bones, such as the bones of the cranium and pelvis, and the epiphyses of the long bones, are not so easily regenerated as those that are denser, such as the cylindrical bones. In several bones,—in the patella, for example,—fractures are often reunited only by a fibrous flexible ligamentous substance.§ The portion of the cranium removed by the trephine is seldom found to be completely replaced by bony matter, even after a great lapse of time; although this sometimes takes place, as in the case witnessed by Scarpa. The reunion of fractured

* Meckel's Archiv. 1830, 4.

† The different facts relative to the reproduction of cartilage will be found in Weber's edition of Hildebrandt, i. 306.

‡ Experiments to ascertain the degree of reproductive power possessed by fibrous membranes have been instituted by Arnemann, Murray, Moore, and Kohler, and are cited by Weber.

§ Otto, Pathol. Anat. p. 225.

bones is effected by the effusion of plastic lymph,—a result of the inflammatory process,—and the conversion of this lymph into bony matter. The new bony substance which unites the ends of the broken bone is at first irregular in form, but is afterwards gradually reduced nearly to the form of the old bone. The fibrinous matter is effused from all the parts which were injured at the time of the fracture, from the bone and the periosteum, as well as from the surrounding cellular tissue and other parts which have become inflamed. The matter first effused is here, as in all inflamed parts, the fibrin which was previously dissolved in the blood; it acquires soon the consistence of jelly, which becomes organised, while, the inflammation going on, the periosteum becomes thickened and the ends of the bone softened. The first exudation here described must be distinguished from the true callus; the matter first effused is the uniform product of inflammation in all parts; the callus is produced by the conversion of that part of the fibrinous exudation which is nearest to the ends of the bone, first into cartilage, and at length into bone. If the two ends of the bone are so situated that they can unite, the callus surrounding them forms one mass; but if they are so far removed from each other that this cannot take place, a separate callus is formed around each. The cartilage runs through the different stages of the formation of bone, it becomes ossified by the deposition of calcareous matter, and at last the cellular structure of bone is developed. Howship found a close red net-work of vessels in the fibrinous effusion as early as the fifth day; and Richerand says that by the twelfth or fifteenth day the bone is in a state of complete inflammation, and itself effuses fresh lymph. The provisional callus not only partly surrounds the portions of bone, but also fills the medullary cavity at the situation of the fracture. The mass, however, which fills the medullary cavity is, according to Professor M. Weber's observation, gradually reduced to cellular septa, and the callus assumes more and more the form of the bone, becoming the "definitive callus." Even after ossification is complete, its form continues to undergo change; and it is not till after some months that the external surface of the mass which unites the formerly separate ends is nearly even, and the internal cavity restored. Villermé* states that the callus has assumed its cartilaginous structure at the end of from sixteen to twenty-five days, and becomes ossified within a period varying from twenty days to three months.

The number of treatises on this subject is very great.† The princi-

* Dict. des Sc. Méd. art. Ossification.

† A full account of the views that have been held relative to the production of callus, will be found in the Dict. des Sc. Méd.; and in A. L. Richter's Handbuch der Lehre von d. Brüchen und Verrenkungen der Knochen, Berlin, 1828, pp. 89—117.

pal point of controversy has been the share which the periosteum is supposed to have in the formation of the callus. Duhamel, Schwenke, Bordenave, Blumenbach, Köhler, Dupuytren, and Boyer, believed that it had an essential share in the process; while even Detlef had pointed out, that the periosteum does not at all contribute to the formation of the callus, and is not formed till after it. Haller, Soemmering, Scarpa, Richerand, and Cruveilheir supposed the callus to originate in an exudation from the ends of the bones themselves. We have already spoken of Duhamel's opinion, that the periosteum is the essential organ for the formation of the bones—an opinion so contrary to the principles of physiology,—and the periosteum alone can as little form the callus as it can form the bone. The periosteum merely contributes with all the other parts injured at the time of the fracture,—as well the bone, as the surrounding tissues which become inflamed,—to the effusion of the first fibrinous matter.

Ossification always commences, it appears from Miescher's researches, at the surface of the bone, and not at the fractured extremities, but at some distance from them, so that an ossified capsule, as it were, is formed around each of the fractured ends of the bone; by the extension of the ossification these capsules become united. The commencement of the ossification at the surface of the bone, and its extension from them, show that the presence of the bone is here necessary to the formation of new bone.

The *serous membranes* are of all textures the most prone to the effusion of the liquor sanguinis of the blood; the reason of this is, perhaps, that they possess the least proper assimilating tissue. Adhesions are, therefore, most frequent in serous sacs. Whether new synovial membranes are formed in the new articular cavities developed around the heads of bone which have remained long dislocated, is at present uncertain, although Meckel, perhaps too hastily, admits such to be the case. The synovia of a new joint may be derived merely from the remains of the old synovial membrane still adhering to the bone.

The cicatrix of a wound of the *skin* which has healed in that stage of inflammation which is accompanied by the effusion of lymph, is more dense than the skin itself; it is sensible, is at first redder than the surrounding skin, at a later period paler; the epidermis covering it is

The principal writers on the subject have been Haller, Element. Physiol. viii. 345. Detlef, in Haller's Op. Min. ii. 463. Troja, De Nov. Oss. Regeneratione Exp. Paris, 1775. Koehler, Exp. circa Regen. Ossium. Gött. 1786. Van Heekeren, De Osteogenesi præternat. Lugd. Bat. Macdonald, De Necrosi et Callo. Edinb. 1799. Dupuytren, Dict. des Sc. Méd. 38. 434. Howship, Medico-Chirurg Transact. vol. vii. and viii. Kortum, Exp. circa Regenerat. Ossium. Lips. 1823. M. J. Weber, Nov. Act. ac. Nat. Cur. 12. 2. Breschet, Recherches exper. sur la formation du Cal. Paris, 1819.

more delicate. Large scars generally result from the healing of those wounds in which a portion of the skin has been lost by the suppurative process. In this case the cicatrix has no hairs; is in negroes, for the most part, colourless at first, but frequently assumes after a time the natural black colour of the surrounding skin.

Solutions of continuity in *mucous membranes* have little tendency to unite, hence in part the difficulties attending the operation for cleft palate and that for wounds of the intestines. In cases of division of the excretory duct of glands, where the divided ends have been kept in contact, regeneration of the duct sometimes takes place and the passage is restored. This fact was first observed by Müller* in three cases of division of the duct of Wharton, and in one of division of the pancreatic duct, in two cases also of division of the vas deferens in the dog and cat. Brodie, Tiedemann, Gmelin, Levret, and Lassaigne have, after tying the ductus choledochus, found the passage restored in some cases. In Tiedemann's experiments† the jaundice disappeared in some instances at the end of ten or fifteen days. The ligature had either cut through the duct and fallen away before the divided edges had united, or coagulable lymph had been effused around the ligature, completing the canal externally, while the ligature perhaps had separated and fallen into the cavity of the duct, and had passed out through it. After the lapse of from thirteen to sixteen days the canal was found completely restored.

Solutions of continuity in *glands* cicatrise, it is true; but the new substance has not the properties of the glandular tissue. The same is the case in the cicatrisation of *muscles*. P. F. Meckel, Richerand, Parry, Huhn, Murray, and Autenrieth, all describe the substance by which divided muscles unite as similar to condensed cellular membrane, and as evidencing no contractility on the application of galvanism.‡ Wounds of the pregnant uterus cicatrise extremely quickly; by the contraction of the organ the wound is soon rendered extremely small. It appears that the external serous covering of the uterus has the principal share in the cicatrisation.§ A new formation of true muscular substance, as described by Wolff,‖ is certainly not admissible. The remarkable fibrous layers on the pleura and pericardium, which I saw in the museum at Heidelberg, certainly resemble irregular muscular fibres

* De Vulner. duct. excret. Tüb. 1819.

† Die Verdauung nach Versuchung. ii.

‡ See Kleeman, Diss. circa Reprod. Partium. Halle. 1786. Huhn, De Regen. Part. Moll. Gött. 1787. Murray, De Reintegrat. Part. &c. Gött. 1787. Autenrieth et Schnell, Diss. de Nat. Unionis Muscul. Vulnerat, Tüb. 1804.

§ See Mayer, in Gräfe und Walther's Journ. 11. 4.

‖ De Format. Fibrar. Muscul. in Pericardio atq. in Pleurâ. Heidelb. 1832.

in appearance, but may nevertheless be merely fibrinous exudations. We know no test for muscular fibres but their contractility.*

The question of the *regeneration of nerves* has been investigated experimentally by Arnemann, Haighton, Prevost, Mayer, Fontana, Michaelis, Swan, Breschet, and Tiedemann; but it is still involved in considerable doubt, on account of several observers having confounded the mere reunion of the divided ends of the nerve, with the question of the possessal of nervous power by the matter forming the cicatrix. To prove the latter to be the case, whether anatomically or physiologically, is extremely difficult. Nerves when divided generally retract somewhat by virtue of the elasticity of their sheath; but the fact of the reunion of the divided ends of nerves when they lie in contact cannot be doubted. The new substance, if it has the properties of nerves, must contain nervous fibres. It appeared to Arnemann† to differ in structure from true nervous substance. Fontana,‡ on the other hand, states that the new substance which united the divided vagus in his experiments on rabbits was similar to nervous substance; but it is impossible that, so early as twenty-nine days after the division of the nerve, the true nervous fibrils could be generated in the cicatrix; for, on examining the new bond of union even after the interval of seven weeks, I was unable to distinguish any nervous fibrils; the new matter seemed still to consist of dense cellular tissue. Prevost§ divided the nervus vagus in a cat and allowed it to reunite, and, on examining the cicatrix after four months, found the nervous fibres continued through it. The assertion of Michaelis|| that, when portions of nerve from nine to twelve lines in length had been cut out, the ends were again united at the end of some weeks by nervous fibres, is very improbable. To determine whether the new substance of the cicatrix was really nervous substance, Meyer¶ and Tiedemann applied nitric acid, which dissolves the sheath of the nerves, but leaves the nervous substance itself. This test, however, is a deceptive one: as far as my experience goes, the minute fibrils of the nerves cannot be recognised by any chemical means of investigation; they must be examined by means of the microscope while in a perfectly fresh state. This is best done by dividing the nerve into its separate bundles while it lies under a simple microscope on a black tablet; and then, having made the several bundles tense, separating them by means of needles into the primitive fibrils, which may thus be easily seen. By this method, which is conclusive, and in fact not very difficult, I examined the cicatrix of the ischiadic nerve of a rabbit which had been divided seven weeks before, but could not satisfy myself with

* See the remarks of Wutzer in Mueller's Archiv. 1834, p. 451.

† Versuche über die Regeneration. Gött. 1797.

‡ Versuche über das Viperngift.

§ Froriep's Not. 360.

|| Über die Regen. der Nerven. Cassel, 1785.

¶ Reil's Archiv. ii. 449.

any certainty of the existence of parallel fibres in the cicatrix, which was a hard mass, apparently consisting of dense cellular tissue. I will relate the experiment in full at a future page.

Experiments of which the object is to ascertain whether sensation and motion are restored in parts after division of the nerves distributed to them, are of great importance; but, unfortunately, most of the experiments hitherto instituted with this view have been deficient in critical accuracy.

Arnemann, who was opposed to the opinion that the nerves are reproduced, once observed, after a cutaneous nerve of the fore paw of a dog had been divided, that sensation was recovered. Descot* observed the same thing in a man who had wounded the ulnar nerve; but his case is not conclusive, for the nerve was not completely divided. I was witness to the extirpation of a tumour of the ulnar nerve from the arm of a young man by Professor Wutzer; the nerve was divided above and below, and 2½ inches of it removed with the tumour. It is clear that the nervous substance could not have been reproduced; and nevertheless, at the end of three or four weeks, sensation gradually returned in the ulnar side of the fourth finger, not in the fifth finger; the return of sensation being evidently attributable to the connection of the palmar branch of the ulnar nerve, which goes to the fourth finger, with a small branch of the median nerve. At the end of eight months the fourth finger had completely regained its sensibility on both sides. Gruithuisen has observed in his own person a gradual but imperfect return of sensation after division of the dorsal nerve of the thumb. A case is related by Mr. Earle† in which a part of the ulnar nerve had been cut out, and in which, in consequence, the little finger at the end of five years was still useless, and the sensations in it very imperfect. In the great majority of Arnemann's experiments the lower portion of the nerve was quite insensible one hundred or one hundred and sixty days after its division.

Among the most remarkable experiments on the reproduction of nerves are those of Haighton, Prevost, and Tiedemann. Haighton‡ divided the nervus vagus on one side of the neck in a dog, and three days afterwards divided that on the opposite side; the dog died, as when both nerves are divided at the same time. In a second dog he divided the second nervus vagus nine days after the first; the dog lived thirteen days. In a third, the nerve of the one side was divided six weeks after that of the other side; the dog remained in a weak state for six months, but lived; at the end of six months the voice had returned, and the tones had become higher. Nineteen months after the nervi vagi were first divided, Haighton again divided both nerves one after the other; the

* Über die örtlich. Krankeiten der Nerven. Leipz. 1826.

† Med. Chir. Transact. 7. ‡ Mem. Med. Soc. v. iii. Reil's Archiv. ii. 80.

animal died on the second day. Richerand repeated these experiments of Haighton with different results. Breschet and Delphech also deny that the nervous substance is regenerated.* Prevost, on the other hand, has confirmed Haighton's experiments; he repeated them on new-born kittens.

In another series of experiments the proof of the reproduction of the nerves consists in the restoration of the power of motion in limbs the nerves of which have been divided. From most experiments of this kind no inference at all can be drawn, unless, as in Tiedemann's case, all the nerves of the limb have been divided. Swann† has made many experiments to determine the result of division of the ischiadic nerve in rabbits, from which, however, no certain conclusion can be deduced. The nerves distributed to the muscles of the thigh come off from the ischiadic plexus and the ischiadic nerve very high up, and are likewise in part derived from the crural and obturator nerves; so that division of the ischiadic nerve in the middle of the thigh, and even higher, paralyses merely the muscles of the leg and foot. Although the animals, therefore, will not be able to step perfectly with the foot in such a case, still they will be able to use the leg from the action of the muscles of the thigh being unimpaired.

Prosecuting the same inquiry, I have in my experiments adopted a different plan, which, if followed, promises to yield hereafter some certain results, although those which I have obtained are not quite decisive. Exp. 1.—I had divided the ischiadic nerve of a rabbit in the middle of the thigh on the 13th of January 1832. At the end of two months the animal still went lame, resting its tarsal joint on the ground. On the 7th of April the ischiadic nerve was laid bare in the animal still living; the divided portions had united, and at the point of union there was a long swelling. The nerve being irritated with a needle above the cicatrix, no contraction of the muscles of the leg and foot were produced, and irritation of the upper part of the cicatrix had as little effect. But when the middle or lower part of the cicatrix, or the nerve below it, was irritated, a contraction of the muscles of the leg, particularly of the peroneal muscles, which were laid bare, was produced each time. The skin of the foot was insensible from the tarsal joint to the toes; the skin of the leg had not lost its sensibility, for it derives its nerves only in part from the portion of the ischiadic nerve which is below the point of division. Exp. 2.—I had divided the ischiadic nerve in a rabbit above the middle of the thigh; at the expiration of one month and twenty days, the animal was still as lame as it was immediately after the operation. I then laid bare the nerve again and the muscles of the leg.

* Lund, Vivisectionen, 218.

† On the treatment of local affections of the nerves, London, 1820, translated into German by Francke. Leipz. 1824.

Mechanical irritation of the nerve with a needle, when applied above the cicatrix, excited no contractions in the muscles of the leg; but, when applied below, it produced contractions, particularly in the peroneal muscles. The galvanic stimulus developed by a single pair of plates was applied to the nerve above the cicatrix, but it had no influence on the muscles supplied by the nerve below the cicatrix. My assistant, Dr. Schwann, now applied the wires of a battery of one hundred pairs of plates to the nerve above the cicatrix, a glass plate having been previously placed beneath it; all the muscles of the leg were immediately thrown into strong contractions. But we found, although not till too late, that such very strong galvanic discharges are transmitted through the nerve as they would be through any other moist animal conductor, and are not adapted to any physiological experiments; for they cannot be isolated, and, as we afterwards observed, are transmitted by a nerve the structure of which is completely destroyed by being crushed, and even pass from one portion of a divided nerve to another through the medium of the moist surface of the body on which they lie. Exp. 3. —On the 10th of July 1832, the ischiadic nerve of a rabbit was divided above the middle of the thigh. After the lapse of six months, during which time the animal still dragged its foot somewhat in progression, the galvanic stimulus of a single pair of plates, and of a weak battery of thirty pairs of plates, excited no contractions in the muscles of the leg, both poles of the battery being applied to the nerve above the cicatrix. We were much astonished, however, to perceive that, even when the wires were applied to the nerve below the cicatrix, or to the peroneal nerve, only the most feeble contractions were excited in the muscles of the leg; particularly in the peroneal muscles, which were exposed. Later experiments, made in conjunction with Dr. Sticker,* have more fully illustrated these results. Too much importance had been attributed to Nysten's experiments,† which showed that, in persons who had died some days after an apoplectic attack, the muscles still retained their irritability—contracted on the application of galvanism,—although the brain had lost its influence; for, in these experiments which I have made with Dr. Sticker, we found that, although the lower portion of a divided nerve retains its irritability for a certain period, still, if the union of the two portions was prevented, the irritability is afterwards lost; so that if at the end of two months the galvanic stimulus of a single pair of plates is applied to the lower portion of the nerve, it produces no contractions in the muscles to which the nerve is distributed. Even when applied to the muscles themselves, the galvanic stimulus in several cases did not excite contraction. The experiments on rabbits related above are, therefore, more in favour of the supposition of reproduction of the nerve than opposed to

* Mueller's Archiv. 1834, p. 202.

† Nysten, loc. cit. p. 369.

it. In the third experiment only the irritability in the lower part of the nerve was almost completely lost, (although the nerve was allowed to unite,) and in this case, therefore, it seems that the nerve had cicatrised, but that the nervous communication was not restored. Since it appears from Sticker's experiments that, unless their communication with the brain is maintained, nerves cannot preserve their irritability for any length of time, the mere fact that the lower portion of a divided and re-united nerve is irritable after the lapse of several months, proves that the union of the nerve restores in some degree the nervous communication.

Schwann has recently performed the following experiment on a frog, which clearly proves the fact of the reproduction of nerves. He divided the ischiadic nerve in the middle of both thighs; after the operation, the frog at first leaped but rarely, generally moving by crawling only; after a month it leaped more frequently, and at the end of three months this movement was performed almost as well as by any other frog. The sensibility of the foot, also, which at first was lost, was at this period nearly entirely restored; and irritation of the nerve with a needle, whether quite high up or close above the cicatrix, produced strong contractions of the muscles supplied by the part of the nerve below the point irritated. Irritation of the nerve below the cicatrix, or of the muscles themselves, had the same effect. The following were the appearances that Dr. Schwann found on examining the divided nerve; only one could be examined: when it was separated from the surrounding parts with which it was connected, in the situation of the wound a portion about one line in length was observed, which had not the brilliant white colour of the rest of the nerve, but was more transparent. This appearance seemed to indicate how far the divided nerve, or at least its neurilema, had retracted; and the portion that presented it was formed, consequently, in part by the nervous matter which protruded from the ends of the divided nerve, and in part by new-formed substance. The whole mass could not be supposed to be formed by the nervous matter pressed out of the divided nerve; it was too long. By the aid of the microscope, however, this part of the nerve was seen to contain nervous fibrils, lying close together and running its whole length, and the transparent aspect seemed only to result from the neurilema being less perfectly reproduced. The fibrils were continuous with those of the two ends of the nerve, and the stretching that was necessary for the microscopic examination fully accounted for the nervous cylinders being, at some points, connected only by very delicate threads. The upper end of the nerve was enlarged, as is the case with the ends of nerves in the stump of amputated limbs; the lower portion did not present the phenomenon.

Without the reproduction of the nervous substance which has been

thus demonstrated by Schwann, the experiments of Haighton, Prevost, and Tiedemann are inexplicable. Tiedemann divided, in a dog, the nerves of the fore-foot and leg, namely, the ulnar radial median, and external cutaneous nerves in the axilla, and at the expiration of eight months observed a return of sensation and motion, which was still greater after twenty-one months; and at last the dog obtained the complete use of the foot again. This experiment is most convincing in reference to the regeneration of nerve. The return of some degree of sensation in transplanted flaps of skin, after the division even of the portion by which it was connected to its original situation, as in the case of the flap of skin turned down from the forehead to form a new nose, is also an argument for the reproduction of nervous fibres. If in such cases no reproduction of the minute nervous fibrils at the surface of union took place, such a portion of skin, after the division of the connecting isthmus, ought to be quite insensible. I learn from the surgeon the most experienced in operations of this kind, Professor Dieffenbach, that the sensibility remains always very inconsiderable in these parts, but that its existence in some degree cannot be denied.

A circumstance, which very much increases the difficulty of imagining the process that takes place in the regeneration of divided nerves, is, that many nerves contain fasciculi of fibres of different kinds,—motor, sensitive, and sympathetic,—of which the first only, as we shall prove at a future page, have power of exciting muscular contractions. In the process of regeneration, therefore, motor fibres ought to unite with motor fibres, and the sensitive fibres with sensitive, which is difficult to conceive of such minute parts. Schwann's principal object in his experiment detailed above was to ascertain whether the union of motor with sensitive fibres could be proved, by the effect of irritating the roots of the nerves in the spinal marrow; whether, namely, irritation of the sensitive roots of these nerves would excite contractions in the muscles of the parts to which the nerves are distributed. With this view he laid bare the spinal cord in the frog, in which both ischiadic nerves had been divided and had reunited, and divided the posterior roots on both sides; no motion was produced in the legs; but when he divided the anterior motor roots, strong contractions of the muscles of the legs took place. This negative result, however, did not prove that no such union of motor and sensitive fibres existed, for it may be that the sensitive nerves are not endowed with the power of communicating an irritation from the centre to the peripheral parts.

The arguments derived from neuralgic cases in support of the opinion of the reproduction of nerves are the weakest of any. After the division of a nerve the extreme branches of which have been the seat of pain, the painful sensations often return. This might be explained simply by supposing that the affection of the nerve reached higher than the point at which

the nerve was divided, or that the cicatrix excites pains in the nerve. The circumstance that these secondary pains are felt in the extreme parts cannot surprise us, for the nervous trunks contain all the separate fibres the extreme portions of which are distributed in the course of ramification to the different parts; and, as all local sensations depend on the distinct connection of each of these fibres with the brain, affections of the nervous stump may excite sensations which will seem to be in the extreme parts. This occurs even when the extreme branches of the nerve are entirely gone, as in amputated limbs. In all the persons that I have examined who have lost limbs by amputation, sensations as if they still retained the limb were never entirely lost. I have questioned such persons twelve or more years after the operation. When the nerves in a stump are pressed for a long time, the patients suffer distinctly the sensation of the arm or leg, the greater part of which has been removed, being "asleep." The belief that these sensations are lost a short time after amputation is an error of medical men, who generally do not watch the patients longer than a few months.

Gruithuisen's observations* on the consequences of the accidental division of the nervus dorsalis radialis pollicis, in his own person, are extremely interesting. The nerve was divided by a large transverse wound, at the posterior part of the second phalanx of the thumb, which reached the bone. The left side of the back of the thumb to the skin under the nail became, in consequence, perfectly void of sensation. During the inflammation of the wound which followed, this portion of the surface became the seat of an enduring, piercing, and burning pain, (evidently dependent on the inflammation affecting the upper portion of the divided nerve,—the sensation in the skin was, as in the case of amputation, only illusory). In the course of a week, when the wound healed, these pains ceased, and the part then became insensible as before. After a time it acquired some sensibility, but of an extremely undefined character. If he closed his eyes, while this part (the extent of which was two inches in length, and three-fourths of an inch in breadth,) was touched, he could not determine at what point of the surface the contact took place, erring in this to the extent of from three to five lines. When he struck the cicatrix, he had the sensation of pricking under the nail. Eight months after these observations were made, the sensation was still quite as imperfect as before. Gruithuisen concludes with the remark, that the sensitive impressions can be transmitted through the cicatrix of a divided nerve, but that they become so dispersed in it that they cannot be transmitted by distinct nervous fibres to the sensorium so as to appear to come from a determinate spot.

Reproduction of brain and spinal cord.—There are no facts to prove that the consequences of loss of substance of the brain and of the spinal

* Beiträge zur Physiognosie und Eautognosie.

marrow are ever completely removed by the reproduction of new substance.

Arnemann, it is true, observed that in a dog, in which from twenty-six to fifty-four grains of the substance of the brain had been lost, the wound was afterwards filled by a new gelatinous yellow mass, which was more readily soluble in water than the substance of the brain. But it is not certain that this new substance was really cerebral matter. Destruction of the superficial parts of the brain, when unattended with compression or irritation, is often followed by no extraordinary consequences. Lesions of the spinal marrow are, as is well known, but too incurable. Wounds of the brain are stated, by Flourens,* to cicatrise very readily, but without the reproduction of nervous substance which Arnemann supposed to take place. There is at first tumefaction of the wounded parts, they afterwards collapse and simply cicatrise. The functions of the brain are frequently restored after such injuries, but when such is the case, it takes place often within a few days after the injury; reproduction of the cerebral substance is certainly not the only cause of it. It is said, however, that when the wall of one of the ventricles of the brain is removed for a certain extent, it is restored by the shooting in of the margins of the opening.

b. Regeneration with suppurative inflammation.

Suppuration, or suppurative inflammation, always ensues when a wound is prevented from healing in the stage of fibrinous exudation or adhesive inflammation. During the process of healing by suppurative inflammation, no effusion of plastic organisable matter takes place,—pus is not susceptible of organisation. Sir E. Home's ideas concerning the conversion of pus into granulations are completely erroneous. Pus is formed by secretion on the surface or in the interior of the inflamed part, and at the moment of secretion, according to Brugmans and Autenrieth, is more fluid and transparent. It appears to be formed at the expense of the organised matter, of which the composition is changed by the inflammatory action. The globules of pus are unequal in size,—for the most part they are larger than the red particles of the blood, with which they have no similarity in form; they are either particles thrown off from the suppurating surface, or, like the particles of other secretions, are formed in the fluid secretion at the moment that it exudes, in a manner similar to that of the formation of globules in solution of albumen at the commencement of its coagulation.

When wounds heal by the first intention, that is to say, in the adhesive stage of inflammation, the margins of the wound are united by the aid of the plastic matter effused from the blood. When they heal by the suppurative process, there is no developement of new vessels in matter

* Expér. sur le Système Nerveux.

previously exuded on the surface, but the suppurating margins and base of the wound advance so as to diminish the size of the wound by the growth of the particles already organised. The opinions of writers with regard to this simple process have been, in some respects, very strange. It is by many supposed that, during the granulation of a suppurating wound, both suppuration and effusion of coagulable matter, which is afterwards organised, take place at the same time; but the occurrence of the two processes at the same time, on one and the same point, is impossible; where one exists, the existence of the other is precluded. The opinion of Langenbeck, that the filling up of an ulcer does not commence till the small vascular elevations or granulations cease to pour out pus, and secrete plastic lymph, is not supported by facts. In a wound which secretes good pus, new substance is formed by the process of growth, so as to diminish the cavity in extent, while at the same time the process of throwing off effete matter—the suppuration—continues; this is matter of frequent observation, and has been found by Pauli to be universally the case. Since, then, the granulations do not result from the previous exudation of plastic matter, the healing of the wound, it appears to me, can only be explained by supposing the organised structure forming the walls of the wound to grow both at the base and circumference by interstitial assimilation—by a process similar to the ordinary growth of all organised parts,* only much more rapid. The diminution of the size of the suppurating wound would thus take place uniformly from all sides,—from the base as well as from the borders. The new matter formed in the cavity of the wound, having a granular surface, has received the name of granulations. In *granulations* there are no free ends of vessels secreting pus,—the blood-vessels have no free ends in any part of the body,—they contain merely reticulated capillaries. The pus, therefore, is not secreted by the open ends of vessels, but by the exposed surface of the granulations. The encroachment of the organised parietes of the wound on the cavity equally from all sides, from the borders as well as from the base of the wound, diminishes its size both in circumference and depth, till it is reduced to a point or quite closed, when the suppuration ceases spontaneously. It is only when the interstitial growth takes place more rapidly at the base of the sore than at the borders that the granulations rise above the surface; and under these circumstances the suppurating wound cannot be reduced till the proper relation between the borders and base of the sore is restored by cauterisation. In the contrary case, when the bottom of the wound is not regenerated so quickly as the margins, the sore becomes sinuous, and requires to be laid open by division of the borders. When the suppuration is very superficial, the secretion of pus ceases simultaneously with the inflammation, without any reduction of the extent of the wound by this growth of the base and margins being necessary.

* See page 375.

Pauli* has given a representation of the microscopic appearance of the capillaries in a suppurating wound.

In cases where a large extent of skin has been lost, it is replaced partly by growth inwards of the skin forming the margins of the wound, partly by the condensation of the cellular tissue, which has been observed in a striking degree in cases of destruction of a large part of the scrotum. When great loss of skin occurs in cases of necrosis, in which the surface of the bone, from which the dead portion is thrown off, becomes soft and gives rise to a granulating growth, as we have observed in a case of extensive loss of substance of the integuments of the cranium, with necrosis of a large part of the external lamella of the cranial bones in consequence of a burn, the substance which forms the cicatrix seems to be formed in part by prolongation inwards of the cutaneous margins, and partly also by the growth of cellular tissue from the surface of the granulating bone, which also forms for itself a new periosteum.

The process which ensues upon *necrosis* of the bones is a subject of great physiological interest.

Necrosis, or the death of a bone, is the consequence either of an unfavourable termination of inflammation of the bone in a bad constitution, or of its vascular supply being cut off by the destruction of its periosteum or medullary membrane. Destruction of the periosteum, to a considerable extent, cuts off the supply of blood which the bone received through the medium of the vessels of the periosteum, and induces the death of the exterior layers of the bone. When the medullary tissue of a bone is destroyed by inflammation, or artificially after a cylindrical bone has been sawn through in an animal, the supply of blood to the internal layers of the bone is in the same way cut off, and their death is the consequence; in neither case does the whole thickness of the bone lose its vitality. The process which ensues in the external parts of the bone when the internal layers are destroyed, and in the internal parts when the external layers become necrotic, is very remarkable. The osseous substance becomes inflamed; the consequence of which is the effusion of coagulable lymph, as in the inflamed ends of broken bones; and this coagulable lymph, as in the case of fractures, becomes organised, and afterwards ossified. If the lesion and consequent necrosis is on the outer surface of a cylindrical bone, the exudation takes place on the inner surface into the cavity of the bone, so that the medullary cavity is diminished in size. The callus thus formed on the inner surface of the bone strengthens it, supplying the loss of substance which it has sustained by the death of its outer layers. If any long bone is sawn across in a living animal, and its medulla destroyed, so as to produce necrosis of the inner layers of the bone, the exudation takes place on the external surface of the exterior still living lamellæ. This is best seen

* De Vulner. sanand. Comment. Gött. 1825.

in the hollow bones of birds, after a hot iron has been introduced into their cavity.

Most writers have confounded the interstitial swelling, or, as Scarpa called it, the expansion of the inflamed bone itself, with the deposition of osseous matter which, in the two cases of necrosis above indicated, takes place either into the medullary cavity, or on the surface of the bone, and which is the result of the inflammatory exudation. The swelling of the bone is seen most distinctly in mammalia, and in them has the chief share in the reproduction of the part lost by necrosis. The exudation is a temporary process, but the swelling of the bone itself continues during the whole course of the inflammation of the bone, and is not very evident until the bone becomes softened and extremely vascular at the part where it is in contact with the dead portion. The surface of the living inflamed bone, where it is in contact with the dead bone, becomes quite soft, red, and granulating; and in internal necrosis the bone becomes enlarged, not from the formation of a new tube around the internal dead laminæ of bone (the sequestrum), but by thickening of the external laminæ which have retained their vitality, or, in external necrosis, by growth of the living bone under the external dead portion, towards the exterior as well as towards the medullary cavity. The increase in size of the inflamed and softened bone goes on while the surface in contact with the dead bone continues to secrete pus, either internally when the necrosis is internal, or externally when the dead portion is external.

If the whole thickness of a bone has died, no new bone can be produced; the periosteum has nothing to do with the reproduction of the bone; but when merely the external or the internal layer has perished, then the bone is usually reproduced: but even in this case an entire new bone is not formed; the cylindrical sequestrum, in the case of internal necrosis, is only the internal laminæ of the long bone, and the new cylinder around it merely the external laminæ of the bone thickened and swollen by interstitial growth.

There has been much contention about the question, whether the new osseous mass which encloses the sequestrum is reproduced merely by the enlargement of external layers of the bones, or is formed by the periosteum itself. Weidmann* supposes that both cases occur. Troja is led by his later experiments to adopt the first opinion, and Scarpa has recently proved it to be correct. Meding, on the other hand, supports the opinion of the formation of bone by the periosteum. It is in itself inconceivable that a membrane, such as the periosteum, which serves merely to contain the vessels which pass from it into the bones, and to invest the latter, can itself form organised osseous substance. I have already given my reasons for not assenting to this opinion. But it

* De Necrosi Ossium.

can be clearly shown in mammalia, which are better adapted for this purpose than birds, that the formation of the new tube of bone is effected partly by the effusion of lymph in the adhesive stage of inflammation on the surface of and by the inflamed bone itself, not by the periosteum; but that the greatest part of the osseous mass is formed by the living layers of bone which surround the inner sequestrum undergoing enlargement, which goes on increasing during the whole period of suppuration. I appeal here to the excellent observations of my colleague, M. J. Weber, which have been made known by M. Bannerth in his interesting thesis, in which drawings from the preparations are also given.

All that I have here said respecting the reproduction of bone was suggested to me by Professor Weber's preparations, by which the correctness of Scarpa's opinion is placed beyond a doubt. Scarpa, however, did not observe the exudation which takes place in the first stage of the process between the periosteum and bone, and which is seen most distinctly in birds; although in them also the spongy enlargement of the bone takes place: in mammalia the enlargement of the bone is most remarkable, but the exudation is also present. In Weber's preparations the periosteum is seen covering the new osseous mass unchanged in its structure, except that here and there it presents a small thickening like cartilage.*

* On the subject of the reproduction of bone attending necrosis, consult Troja, Neue Beobacht. ü Vers. über die Knochen: übers. von Schönberg. Erlang. 1828. Köhler, Exp. circa Regen. Ossium. Gött. 1786. Kortum, loc. cit. Meding, Diss. de Regen. Ossium. Lips. 1823. Scarpa, über die Expansion der Knochen und den Callus. Weimar, 1828. Bannerth, Naturæ Conaminum in oss. læs. sanand. indagatio Anat. Physiol. Bonnæ, 1831. The best account of all previous researches on the reproduction of the tissues will be found in the prize essay of Pauli, cited above.

SECTION III.

Of secretion.

CHAPTER I.

OF THE SECRETIONS IN GENERAL.

During the passage of the blood from the minute arteries through the capillary system of vessels into the radicles of the venous system, a part of the "liquor sanguinis" with the matters dissolved in it is imbibed by the tissues,* by the agency of which it undergoes a chemical change; some of its components are extracted from it, while it receives in exchange other matters derived from the parenchyma itself.

The changes which the organic matter suffers in this way may be termed generally transformations or "metamorphoses." They are of three kinds:

1. Transformation of the components of the blood into the organised substance of the different organs,—"*intus-susceptio*," or nutrition, which has been treated of in the preceding section.†

2. Transformation of the components of the blood on the free surface of an organ into a solid unorganised substance, which is the mode of growth of the non-vascular textures,—"*appositio*."‡

3. Transformation of the components of the blood into a fluid matter, which escapes on the free surface of the organ,—secretion, which is the subject of the present section.

The matters separated from the blood by the action of a secreting organ are,—1. Substances which existed previously in the blood, and are merely eliminated from it: such are the urea, which is excreted by the kidneys; and the lactic acid and its salts, which are components both of the urine and of the cutaneous perspiration. These are called *excretions;* the process of their separation from the blood, *excretion*. The excretions which are met with most generally in the animal kingdom, namely, the urine, and the fluid perspired by the skin, are in the human subject acid; but all excretions are not acid, as Berzelius formerly supposed, for the urine of some herbivorous animals is alkaline, as are also some of the excretions peculiar to several animals; for instance, the acrid matter excreted from the skin of the toad. 2. Substances which cannot be simply separated from the blood, since they do not pre-exist in it, which, on the contrary, are newly produced from the proximate components of the blood by a chemical process; such are the bile, the semen, the milk, mucus, &c. These are called *secretions*.

* The laws which regulate the imbibition of fluids by organic tissues have been already detailed at page 242.

† See page 360.

‡ See page 384.

These true secretions are again divisible into two series:

a. Some either fulfil no further purpose in the animal economy by which they are formed, or at most serve for its defence by being poisonous to other animals, or attract or repel other animals by diffusing peculiar odours. Secretions of this kind may have their seat at almost any part of the surface of the animal body. As examples, we may instance the acrid secretions of many beetles, of wasps, bees, and the scorpion; the peculiar secretions of spiders, insects, and muscles; the ink of the cuttle-fish; the castoreum of the preputial follicles of the beaver; and the secretion of the musk-bag, situated under the skin of the abdomen above the penis, and opening in front of the prepuce in the musk-deer.*

Besides their action out of the system, such secretions may have an importance in the economy of the animal which forms them, inasmuch as, being formed at the expense of the proximate components of the blood, their production must be attended with a change in its composition, and the suppression of them would, in some cases perhaps, be equally as injurious to the system as the suppression of certain morbid discharges in the human body, which are to be regarded as means of preserving the healthy constitution of the blood. In the case of the conversion of one organic compound into another out of the body, certain elements which are not necessary to the new compound are set free; for example, during the generation of alcohol from sugar carbonic acid is disengaged. The production not merely of the cutaneous exhalation and of the urine, but also of the peculiar secretions of many animals, may be explained in a similar manner. The formation and elimination of the urea have the same relation to the production of higher organic products, as the evolution of carbonic acid has to the formation of alcohol from sugar. If morbid secretions are regarded in the same point of view, they must be distinguished into two kinds; first those, the elimination of which is absolutely necessary for the preservation of the normal constitution of the blood, and which cannot with impunity be checked, unless the process of sanguification generally has previously undergone a favourable change; and, secondly, those morbid secretions which are merely the result of local conditions, and may be arrested without fear. After amputation of a part which has been the seat of a copious but not cachectic suppuration, a surgeon is not justified, therefore, according to physiological principles, in instituting vicarious discharges, or in preventing the healing of the wound by the first intention.

b. Other secretions, such as the milk, bile, semen, and mucus, serve further purposes in the animal economy.

The true *secretions* are frequently alkaline, but by no means always so; and one and the same secretion (we may instance the saliva or pancre-

* For an account of these and many other analogous glands, see J. Müller, De Glandul. secernent. tructurâ penitiori. Lipsiæ, 1830.

atic fluid) often alternates from the acid to the alkaline state under the influence of trifling circumstances.*

The formation of any one of the peculiar *secretions*, the essential proximate constituents of which do not exist in the blood itself, presupposes the operation of a special chemical apparatus, whether this be a membrane or a gland. The destruction of the secreting apparatus must put a permanent stop to the secretion; thus the semen can no longer be formed after the removal of the testes, nor the milk after the extirpation of the mammary gland. Haller's assertion,† that almost all secretions may, under the influence of disease, be formed by each and every secreting organ, is incorrect. Such a phenomenon would be totally different from the cases in which the secretion continues to be formed by the natural organ, but, not being able to escape towards the exterior on account of some obstruction, is re-absorbed into the blood, and afterwards discharged from it by exudation in other ways. The *excretions*—those matters which exist ready formed in the blood, and of which urea is an example,—can alone, after the destruction of the excreting organ, be eliminated from the vessels in all parts of the body by the process of exudation.‡

Secreting apparatus.—The apparatus for the formation of the animal secretions are either cells, such as those of the adipose tissue; plane membranes, such as the synovial and serous membranes; or organs of peculiar complex structure, the glands.

1. *Secreting cells.*—The cells of the ovary—vesiculæ Graafianæ—filled with an albuminous fluid in which the much more minute ovulum is developed, and the cells of the testes of some fishes,—of the eel and small lamprey, for example,—in which the testis has no seminal or efferent duct, as Rathke first observed, and in which the semen escaping by rupture of the cells into the abdominal cavity is evacuated from it again by a single orifice, are instances of secreting cells. Secretion by cells is, however, observed to the greatest extent in the adipose cellular tissue. This is the occasion for making some remarks on cellular tissue generally.

The cellular tissue, which might, by reason of its forming the connecting medium of other tissues, be termed "connexive tissue,"(bindgewebe,) has latterly become one of the most enigmatical of the animal textures, in consequence of physiologists having begun to adopt the opinion of Borden, Wolff, and Meckel, who regarded it as a kind of mucus filling the interstices of the texture of organs, and supposed that its apparently membranous and cellular structure is produced by the action of the air, by traction, or by the infiltration of fluid. These suppositions have received support from the circumstance of the soft condi-

* Schultze has given a detailed account of the acid or alkaline reaction of the different animal fluids in his Vergleichende Anatomie.

† Element. Physiol. ii. 369.

‡ See page 151.

tion of the cellular tissue in the embryo. It has indeed been imagined, though without any reason, that all the organs of the body are developed in the embryo from cellular tissue. But the germinal nidus, in which an organ is formed in the embryo, and which we have named "blastema," has much higher properties than cellular tissue,—is endued with creative powers,—and is of a totally different nature. Thus, in the developement of the glands we see the blastema in the form of a gelatinous semi-transparent matter, in which the ramification of the secreting tubes commences in an arborescent form, and is extended by the protrusion of new branches; while the blastema, which constitutes a kind of atmosphere around the secreting tubes, is at first of considerable extent, but is absorbed in proportion as the tubes become more ramified and numerous. In the lobulated glands,—the lachrymal and salivary glands,—the blastema itself likewise becomes lobulated in the progress of developement of the gland.*

The incorrect notions relative to the formation of cellular tissue owe their origin to anatomists having neglected the microscope in the investigation of its structure, or to their having used imperfect instruments. The ultimate elements of all cellular tissue are fibres; never either globules or lamellæ. Even the membranes which form the cells of the adipose tissue are first composed of fibres. The primary fibres of cellular tissue, which were known to Treviranus and Krause, are among the most minute constituent elements of the human body. Their diameter is, according to Krause, from $\frac{1}{3230}$ to $\frac{1}{1100}$; according to Jordan, $\frac{1}{1430}$ of an English line. It requires a magnifying power of four hundred diameters to recognise them. They are transparent, and their edges quite smooth; in which characters, as well as in yielding gelatin by boiling, they resemble the primitive fibres of tendons. The fibres of the cellular tissue are united, so as to form lamellæ and small membranes; and these lamellæ, or bundles of fibres, cross each other in all directions, producing an irregular interlacement, of which the interstices communicate, as is easily proved by inflation. This last circumstance, and the whole structure of the cellular tissue, distinguish it from the corresponding tissue of vegetables, which is formed of, for the most part, angular closed cells.

Cellular tissue is divided into the serous and adipose. The opinion that the cellular tissue is essentially composed of reticulated lymphatic vessels, is rendered improbable by the circumstance of the direct transition of the cellular tissue into the fascia superficialis, the ultimate elements of which are exactly similar to those of cellular tissue.†

* See J. Müller, De Gland. Struct. Penit. tab. vi. figs. 11, 12; tab. v. fig. 8.

† These remarks on the structure of cellular tissue are extracted from a paper by Dr. Jordan on the Tunica Dartos and the allied tissues, in Müller's Archiv. 1834, p. 410. I may remark that I have verified his observations.

The fat is merely a deposit in the cells of the cellular tissue. It is met with in the subcutaneous cellular tissue, in the omentum, around the kidneys, in the medullary cavity and cells of bones, and less extensively in several other parts. A special structure appears not to be necessary for its secretion, since it can be deposited in all parts. It is quite unorganised, and at the temperature of the human body is even fluid or soft. The different kinds of animal fat are chiefly distinguished by the different degrees of temperature at which they become fluid or soft, and by the different proportions of stearin and elain which they contain. Human fat is among the softer kinds. The adipose matter of cold-blooded animals is still fluid at ordinary temperatures. The chemical composition of fat has been already stated.* The use of the fat evidently consists partly in contributing to preserve the proportions of the external form, and partly in protecting the internal parts by virtue of its being a bad conductor of caloric. But the fat may likewise be regarded as a deposit of nutriment, which during fasting, and also during wasting of the body, is again easily dissolved by being united with other animal matters, or by being converted into a saponaceous state, and having thus again entered the circulation, is applied to the formation of other organic compounds.

2. *Secreting membranes.*—The principal secreting membranes are the serous membranes, the mucous membranes, and the skin.

a. The serous membranes seem to be formed of fibres like those of cellular membrane, aggregated in the same way into bundles, which are interwoven together. There are three orders of serous membranes: 1. The synovial bursæ, of which some are subcutaneous, while others either surround or are situated beneath tendons, and give them an investment. 2. The synovial membranes of joints, which likewise invest the tendons or ligaments that pass through their cavities. (The synovia is an alkaline albuminous fluid, which coagulates at the boiling temperature.) 3. Serous membranes which line visceral cavities. These are closed sacs, and originate in the free surfaces of viscera where they come into contact with each other, or lie in cavities unattached to surrounding parts, becoming a membranous coat. The viscera which are invested by a serous membrane, are, as it were, pressed into the shut sac which it forms, carrying before them a portion of the membrane, which serves as their investment. To the law that serous membranes form shut sacs there are but few exceptions, viz.: the opening of the Fallopian tubes into the abdominal cavity,—a structure which exists in man and all vertebrata, with the exception of a few fishes; and the openings by which the abdomen in fishes communicates with the exterior,—in the sharks and rays double, in the eel and lesser lamprey a single opening. In the sturgeon, sharks, and rays, the pericardium and peri-

* Page 132.

toneum communicate; but the communication between the two cavities is most free in the ammocœtes and myxinoid fishes.*

Many have imagined that the serous cavities during life contain a gas, without once inquiring what kind of gas could exist there. The supposition is erroneous. The serous membranes are during life so filled with the viscera, that there exists no space unoccupied; and only just so much fluid is secreted by the membrane as is necessary to lubricate the contiguous surfaces, and to prevent adhesions. By the constant action of the abdominal muscles the viscera of the abdomen are kept closely pressed together: any change of capacity which the abdominal cavity undergoes must depend on the varying fulness of the intestinal canal. Between the pleura costalis and pleura pulmonalis there is likewise during life not the smallest space; for the surfaces of the lungs follow constantly the movements of the thoracic parietes, on which, indeed, (the motion of the lungs with the thoracic parietes) respiration depends. There is also no necessity for supposing the existence of any gaseous matter between the heart and pericardium during life, for one part of the heart is always distended with blood, while the other part is contracted; and even if a vacuum could be produced in the pericardium by the contraction of one part of the heart, the lungs on each side would, by the pressure of the external air in the bronchi, be forced in to fill it up.

There subsists between the serous sacs such a sympathetic connection, that inflammation in one is readily communicated to the others. A disease peculiar to them is the effusion of the serum of the blood, and it frequently occurs when the viscera invested by them are the seat of organic disease.†

The mucous membranes consist of an interlacement of fibres, on which [in some parts?] a stratum of very minute perpendicular cylinders rests, and in which numerous mucous follicles are seated. The intimate structure of the epithelium, as well as that of the epidermis, have been brought to light by the observations of Leeuwenhoeck, Raspail, Purkinje, Valentin, and Henle. The epithelium consists of minute portions, arranged side by side like a pavement; the particles, each of which contains a nucleus, are being constantly thrown off, and are therefore seen in the saliva and mucus of the mouth, when they are examined

* It is an error to suppose that the viscera of the abdomen of birds are contained in the air sacs, which in these animals descend on each side of the abdomen, and communicate with the bronchi by openings on the surface of the lungs. According to my observation, both lobes of the liver and the greater part of the intestinal canal lie in separate compartments of the abdominal cavity between the lateral air sacs, and distinct from them. Air forced into the bronchi distends the air sacs, but not the visceral cavities of the abdomen.

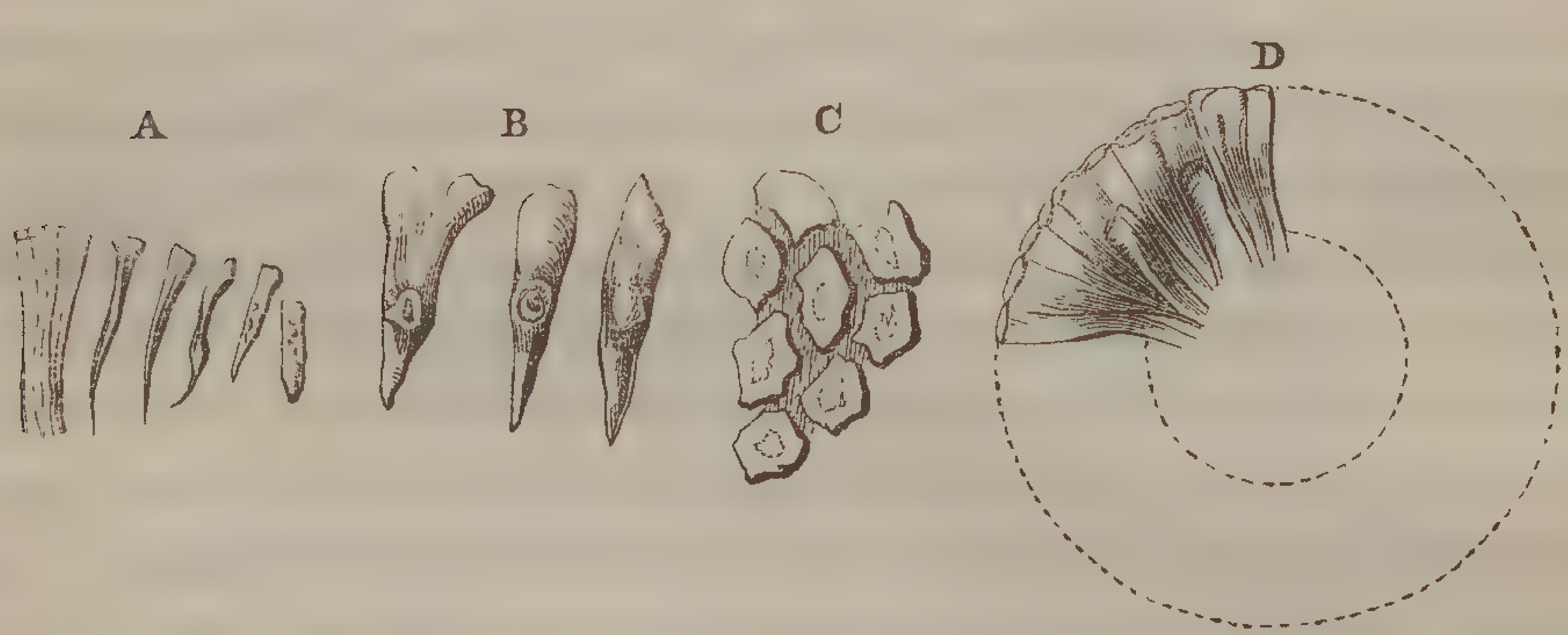
† For remarks on the vascularity of serous membranes, see page 214.

with the microscope. In some parts, as in the mouth, the particles of epithelium are thin scales (fig. 31, B) lying horizontally one over the

Fig. 31.*

other, so as to form strata. [Dr. Henle finds that the particles of epithelium which form the deeper layers are smaller, but at the same time thicker, like vesicles; they also contain a nucleus, (fig. 31, C,) and appear to be the same bodies as the scales, but not yet flattened; (their arrangement is seen in the section of conjunctiva, fig. 31, A, where the dark shade has the place of the mucous membrane itself.)] In other mucous membranes, as in the intestinal canal, the particles of epithelium are

Fig. 32.†



minute cylinders, (fig. 32, A B,) arranged side by side, like basaltic columns; each cylinder, like the flat scales, containing a nucleus. The villi themselves are covered with these bodies (fig. 32, D). The appearance produced by the nucleus when the free extremity of the cylinders is viewed, (fig. 32, C,) has given rise to the incorrect opinion of the existence of openings on the surface of the villi.

* [Fig. 31. Scales of the epithelium :—B. Scales taken from the inner surface of the cheek ; the margin of one is folded, a frequent appearance of these scales, showing their thinness and flexibility ; C. the more deep-seated or recently-formed scales or cellules from the human conjunctiva ; A. section of the epithelium of the conjunctiva, some scales loosened. The last two figures are copied from Dr. Henle's paper, Symbolæ ad Anat. villor. intestin., imprimis eorum epithelii et vasorum lacteorum.]

† [Cylinders of the intestinal epithelium, after Dr. Henle :—A. Cylinders from the cardiac region of the human stomach ; B. the same from the jejunum ; C. cylinders of the intestinal epithelium viewed by their free extremity ; D. ditto, as seen in a transverse section of a villosity.]

The mucous membranes line all those passages by which internal parts communicate with the exterior, and by which either matters are eliminated from the body or foreign substances taken into it. They are soft and velvety, and extremely vascular. In their chemical properties they appear to differ essentially from the skin; for they yield no gelatin by boiling, are wholly insoluble in water, and the only effect of long boiling is to render them hard and brittle. Their basis, or proper texture, would seem therefore to belong to the albuminous structures.* The external surface of the mucous membranes is attached to various other tissues: in the tongue, for example, to muscle; on cartilaginous parts, to perichondrium; in the cells of the ethmoid bone, in the frontal and sphenoid sinuses, as well as in the tympanum, to periosteum; in the intestinal canal it is attached to a firm membrane or fascia, (the tunica propria of the intestines,) which on its exterior also gives attachment to the muscular fibres of the third coat of the intestines.

The mucous membranes may be distinguished into several principal tracts: 1. The mucous membrane of the nose, from which prolongations are sent into the sinuses communicating with the nostrils; and which, through the medium of the lachrymal canal and puncta, is continuous with the conjunctiva of the eye and eyelids. The conjunctiva is as certainly a mucous membrane as any other of which the character has not been doubted. It participates in the diseases of the mucous membranes, as well the chronic blenorrhæa as the catarrhal affections; and in every case of violent catarrh of the mucous membrane of the nose, the conjunctiva is affected in both stages of the disease. On the other hand, it has nothing in common with the serous membranes, either in the secretion,—for the limpid secretion of the eyes is derived from the lachrymal gland,—or in its form, which is not that of a closed sac.

2. The mucous membrane of the mouth; which communicates in the throat with that of the nose, and sends a prolongation through the Eustacian tube to line the tympanum, and the inner surface of the membrana tympani. In the mouth, moreover, it sends prolongations into the excretory ducts of the salivary glands; and in the pharynx divides into two great branches, of which the one lines the air tubes, and the other the alimentary canal. The mucous membrane of the air tubes ends by lining the air vesicles of the lungs; while that which is continued into the alimentary canal, besides investing it through its whole extent, also sends processes into the ducts of the pancreas and liver. In birds it communicates in the cloaca with the next tract of mucous membrane.

3. The mucous membrane of the generative and urinary apparatus. This lines the whole of the urinary passages from their external orifices to the calices of the kidneys, and in the organs of generation extends

* [See Appendix to the chapter on Nutrition.]

in the form of a lining membrane into the ducts of these organs, and in the female becomes continuous with the serous membrane of the abdomen at the fimbriæ of the Fallopian tubes.

In fishes all the mucous membranes are brought into relation with each other through the medium of the mucous surface of their skin.

A remarkable sympathy is observed to exist between all the mucous membranes; thus their diseases, particularly the mucous discharges, and the catarrhal affections, have a great tendency to spread in them. By virtue of this sympathy the state of one part of these membranes may be ascertained by examining another part; the state of the mucous membrane of the tongue indicates the condition of that of the stomach and intestinal canal. All the mucous membranes have likewise an extraordinary sympathetic connection with the respiratory movements.*

The diseases peculiar to these membranes are the blenorrhæa or mucous discharge, and the catarrhal affections, which are distinguished from the former by their acuteness, that is, the rapidity of their increase and decline, and by their having two stages,—the first, that of congestion,—the second, that of increased secretion.

Mucus is secreted by the lining membranes of the maxillary, frontal, and sphenoidal sinus, and of the tympanum, which have no follicles, as well as by those membranes which have them. The follicles, therefore, cannot be the sole source of the mucous secretion. These follicles or glands, moreover, are merely sac-like depressions of the mucous membrane. In those membranes which are covered with epithelium, by which, therefore, another secretion besides mucus is formed, the latter would seem to be generated solely in the follicles.

Mucus is formed by no other than mucous membranes. It is intended as a protection to the surfaces which are exposed to external influences. It swells when placed in water, but is not soluble in it; does not coagulate by heat; is precipitated from water, in which it is diffused, by alcohol; but, after being washed, can be again diffused in the water. The secretion of all the mucous membranes, however, is not exactly the same; for, as Berzelius found, the mucus of the gall-bladder is quite insoluble in acids, while that of the urinary bladder is to a certain extent soluble in dilute acids, as well as in dilute alkalies. Ordinarily, acids dissolve a very small proportion of mucus. Gmelin states that the mucus of the intestines is coagulated by acids, even by acetic acid. The acids extract very little of it, and do not dissolve it, even at the boiling temperature. The little that is dissolved by the acids, or that is extracted by digestion in water after the acid is poured off, is precipitated by infusion of galls, but seldom by ferrocyanuret of potassium.

c. *The skin.*—The proper cutaneous tissue, in which several organs of different kinds are imbedded, consists of fibres interwoven in all

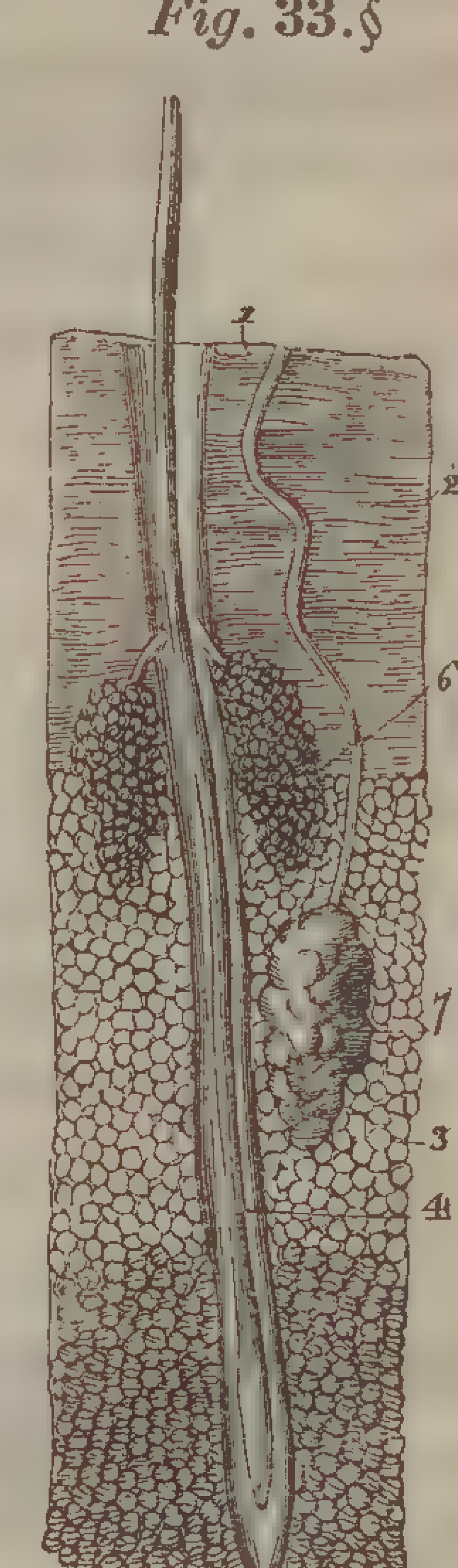
* See page 351.

directions. The surface of the skin presents little elevations,—papillæ,—which are invested by the rete Malpighii and epidermis. By long-continued (twenty hours) boiling, the skin is reduced wholly, or for the most part, into gelatin.* By the property which this substance—gelatin—possesses of forming with tannin a compound which resists putrefaction, is explained the process of tanning.

The skin is the seat of very various secretions, for each of which it is provided with a special organ.

The epidermis, which is the most general of these secretions, is formed in layers by the most superficial stratum of the true skin. The epidermis, like the epithelium of the mouth, consists of minute plates or scales, in the centre of each of which is a nucleus. [The last-formed, and, as yet, soft layer of the epidermis, or the rete Malpighii, consists, according to Henle, of oval bodies like cells or vesicles.] When the skin is coloured, as in the negro, the seat of the pigment is the rete Malpighii which then contains coloured vesicular bodies. The inner surface of the cuticle presents numerous depressions, corresponding to the papillæ of the skin, and the interstices of these depressions have of course a reticular form; hence the name "rete."† Most observers agree that the cuticle is not organized. Schultze has injected with oil of turpentine a very delicate network of vessels which separated with the epidermis from the true skin; but these vessels may have belonged to the sub-epidermic layer, and have been mechanically torn away. Schultze states that they have a diameter several times less than that of the blood globules. If this measurement was not made after the epidermis had been dried, it would afford the proof of what is at present a mere hypothesis,—namely, the existence of vasa serosa.‡

Fig. 33.§



The hair is secreted in the hair follicles.

The sebaceous matter of the skin is secreted by the innumerable minute branched follicles opening by a narrow orifice—folliculi sebacei—which are distributed over its surface. These sebaceous glands (fig. 33, 6,) generally open into the follicle of the hairs.*

The perspiration, lastly, is formed by small tubes of peculiar con-

* [See Appendix to the chapter on Nutrition.]

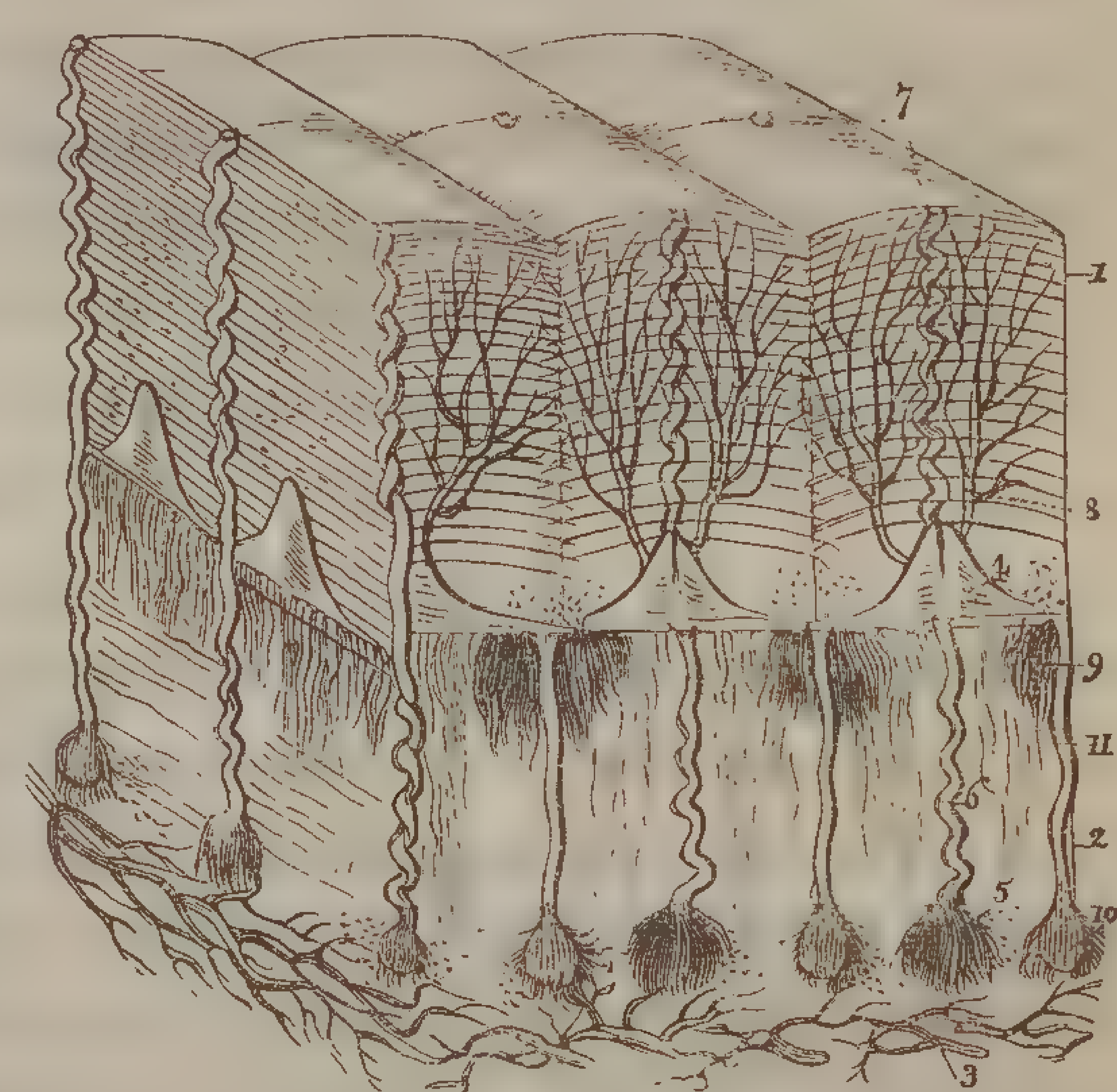
† On the growth of the epidermis and the rete Malpighii, see page 385.

‡ See Müller's Archiv. für Anat. und Physiol. page 30.

§ [Sebaceous and sudoriferous glands of the skin, after Gurlt:—1. The thin cuticle; 2. the cutis; 3. adipose tissue; 4. a hair in its follicle (5); 6. sebaceous gland, opening into the follicle of the hair by an efferent duct; 7. the sudoriferous gland.]

formation, which are spread over the whole surface of the body, and pour out their secretion by minute pores in the epidermis. These sudoriferous organs were discovered by Purkinje and Breschet.† The pores, which are seen along the elevated lines on the skin of the palm of the hand and sole of the foot, are the openings of thread-like organs which traverse in a spiral course (fig. 34,) the epidermis and stratum Malpighianum, enter deeply into the cutis, and terminate in a gland which is formed of a convoluted tube. (fig. 33. 7.) In the parts of the skin where the epidermis is thin, the canals themselves are thinner, and more nearly straight in their course. (fig. 33.) For the purpose of seeing the sudoriferous organs, a piece of skin—that of the palm of the hand is best—should be hardened in solution of carbonate of potash, and, from this perpendicular lamellæ cut with a sharp knife in the direction parallel with the furrows of the skin; in the thin lamellæ the spiral canals and glands may then be seen with the aid of the microscope.

Fig. 34.‡



From this account of the secretions formed in the skin, it results that for each, although it appears only in the form of minute points, a special complicated apparatus is necessary; and that, although the statements of the older anatomists are correct as to the perspiration being poured out by distinct pores, yet the opinion cannot now be admitted that it is

* Gurlt, in Müller's Archiv. 1835, 399.

† See Wendt, de Epidermide Humanâ. Diss. inaug. Vratisl. 1833; and in Müller's Archiv. 1834, p. 280. Breschet, Ann. d. sc. nat., Sept. Oct. Dec. 1834; and Nouv Recherch. sur la structure de la Peau, par Breschet et Roussel de Vauzème; and Gurlt, loc. cit.

‡ [Copy of Breschet's diagram of the structure of the skin:—1. The layers of the cuticle; 2. the cutis; 3. vessels and nerves entering or issuing from the skin; 4. the papilla; 5. the sudoriferous gland; 6. its spiral duct; 7. the funnel-like openings of the sudoriferous organs on the ridges of the cuticle; 8. inhalent vessels in the cuticle; 9. the chromatogenous organ, supposed by M. Breschet to secrete the colouring scales of the cuticle; 10. the gland; and 11. the duct of the blennogenous apparatus, destined, according to M. Breschet, for the secretion of a mucus which, after being mixed with the scales, hardens, and forms the cuticle. M. Breschet has himself more recently renounced his opinion as to the existence of the inhalent vessels with free extremities in the cuticle. (See his Système Lymphatique.) Other observers have not succeeded in finding any distinct structure corresponding to his appareil chromatogene; and the blennogenous organs are probably, as M. Gurlt observes, merely sudoriferous glands, of which M. B. has failed to trace the duct through the cuticle.]

directly effused by open branches of blood-vessels; on the contrary, each perspiratory pore is merely the external opening of a canal leading to a convoluted tube or follicle, which has no other opening, and, like other glands, forms its secretion on its internal surface.*

3. *Glands.*—Of the organs which have hitherto been called glands, some have no ducts leading from them, others are provided with special efferent tubes to carry off the secretion which they form.

The action of the *first kind* of these organs consists merely in their exerting a certain plastic influence on the fluids which circulate through them. They consist, therefore, almost wholly of vessels; they are *vascular ganglia* ("Gefäss-knoten"); the vessels entering them undergo a most minute division, and then again unite to form the efferent vessels, or vessels which return the fluid to the general circulation.

The glands of this kind may be divided into two series:

a. Those formed essentially of blood-vessels,—*ganglia sanguineo-vasculosa.* Such are the spleen in the chylopoetic system, the suprarenal capsules in the genito-urinary system; the thyroid and thymus bodies in the respiratory system of organs, the glandula choroidalis in the eye of fishes, and, lastly, the placenta of the fœtus.

All these organs are masses of blood-vessels, and seem destined merely to exert an influence on the blood which is distributed in such minute channels through their parenchyma. They are sometimes united in one mass, as the placenta and spleen; sometimes divided into several, as the cotyledons and splenculi.

b. Lymphatic ganglia,—*ganglia lymphatico-vasculosa.* These are formed of the branches of the inferent and efferent lymphatics, the ultimate divisions of which form a mass of reticulated vessels and cells. Such are the lymphatic and mesenteric glands. Their action, likewise, can only affect the lymph or chyle which traverses them. They also are sometimes distinct and many in number, like the mesenteric glands, in most cases; and sometimes united into a mass, as the pancreas Asellii, which consists of conglomerated mesenteric glands.

All these glands, which are glomeruli of blood-vessels or lymphatics, are excluded from consideration in the present inquiry.

Glands of the *second kind* not merely produce a change in the fluid which circulates through them, but also give rise to a new fluid, which is the product of a transformation of the blood, and is poured into special tubes or efferent ducts. The structure of all the glands of this kind must now be examined.

* On the chemical composition of the cutaneous secretion, see the Section on the *Excretions.*

CHAPTER II.

OF THE INTERNAL STRUCTURE OF THE GLANDS.

Historical account.—The research into the intimate structure of glands was originated by the *Exercitationes de structurâ viscerum* of Malpighi, published in 1665. The doctrine there laid down by that great anatomist was, that the elementary parts of all glands,—the so-named acini,—have the same structure as the simple follicles and the conglomerated follicular glands; that is, that they consist of minute roundish sacs which receive the secretion from the blood-vessels, and pour it into the efferent ducts. He supported this view by reference to the sacculated structure of some simple glands, such as the pancreas of fishes, and the liver of crustacea, and the process of developement of the liver of the embryo. His theory was founded on good general views, but in the details he was in error; for the essential elementary parts of the compound glands were still unknown to him; each of the parts which he described as follicles of the liver and other conglomerate glands, is an aggregate mass of many of the real elementary parts which are much more minute. It is not surprising, therefore, that confidence in this doctrine was greatly shaken when Ruysch, in 1696, was enabled by his improved method of making minute injections to show, without difficulty, that the so-called follicles of the conglomerate glands contain a vast number of minute blood-vessels. Ruysch, however, attributed too much importance to his method of investigation, and to the facts which it enabled him to discover; and he was thereby led to the false conclusion that the proper substance of glands consists solely of blood-vessels, and that the minute blood-vessels terminate by direct inosculation in the ducts of the glands. This doctrine acquired great weight from the circumstance of Haller being inclined in its favour.* Haller, and several of his followers, have adduced, as arguments for the correctness of Ruysch's view, the escape by the ducts of fluids injected into the blood-vessels of glands, and the occurrence of hemorrhage from secreting tissues. It cannot be denied that, when force is used in injecting the vena portæ, some of the injected matter does sometimes, although rarely, enter the hepatic duct; and in rare instances, after injection has been forced with violence into the renal arteries, some of it is found in the pelvis of the kidney. But, on examination in such cases, it is always found that laceration must have taken place, for the minute branches of the ducts are seen not to be injected, which they should be if the injected fluid had passed directly from the minute arteries into the minute ducts of the gland. My investigations have shown, also, that, whenever during injection of the ducts, whether of the liver, or

* Element. Physiol. lib. xi. section xxiii.

kidney, the blood-vessels become filled; the minute ducts themselves have not received any injection; consequently, that extravasation must have taken place. The escape of fine injected fluids on the surface of mucous membranes, in which no open ends of blood-vessels have been demonstrated, observation having shown in them merely a network of capillaries, is to be explained in the same manner. Hemorrhages, which, moreover, are of exceedingly rare occurrence in glands, are likewise to be referred to extravasation. The kidneys appeared to afford the most evident proof of the communication between the arteries and ducts of glands; indeed, long vessels running in the medullary portions of the kidney, and filled with injection matter thrown into the artery, were shown at anatomical lectures to demonstrate the existence and course of the canals or ducts of Bellini. But a more accurate examination by Huschke and myself has discovered that such vessels are not ducts, but blood-vessels.*

The means of investigation which had hitherto been employed were not adequate to the decision of the question. Other modes of proceeding were necessary, such as the injection of the minute ducts themselves from their principal trunk, and an examination of the whole series of glands with reference to the minute structure, and the origin of their ducts. The investigation of the structure of the kidneys by Ferrein† was the first in which an improved method of examination was adopted and instituted with accuracy. Ferrein discovered the convoluted canals of the cortical substance of the kidney, of which neither Malpighi nor Ruysch had suspected the existence, and which Ferrein regarded as the seat of the secretion of the urine. The similarity of these uriniferous canals, discovered by Ferrein, to the tubuli seminiferi of the testis, which differ from them merely in being visible to the naked eye, was immediately recognised. The tubuli seminiferi themselves, however, must always have been of great importance for the question of the minute structure of glands, since they present to us distinctly an example of the independent existence of the secreting canals, on the parietes of which none but the most minute arteries ramify, and terminate in a capillary network from which the minute veins take their rise. Schumlansky‡ followed up the researches of Ferrein, but he introduced a great error into the description of the minute structure of the kidney; inasmuch as he regarded the acini of Malpighi, which are visible by the naked eye in the cortical part of the kidney, as the seat of the urinary secretion, and supposed that the convoluted urinary canals take their rise in them. He has represented the secreting tubes of the kidney arising very distinctly from the acini, which later researches have shown

* See page 454.

† Mém. de l'Acad. Roy. de Sc. de Paris, 1749.

‡ De structurâ Frenum. Argentorat. 1788.

to consist merely of small plexuses of arteries, and to be quite unconnected with the secreting canals.

Mascagni and Cruikshank next showed that the secreting canals in the mammary glands commence in the form of cells; and Prof. E. H. Weber* has discovered that the same is the structure of the salivary glands of birds and mammalia, and of the pancreas of birds. The interesting researches of Weber, and the equally excellent observations of Huschke† on the structure of the kidneys, were the first step in an inquiry which I have myself since undertaken in its whole extent, having in its prosecution examined the structure of the secreting canals in all kinds of secreting glands.‡ The result has been the discovery that the secreting canals in all glands form an independent system of tubes; that, whether they be convoluted as in the kidney and testis, or ramified in an arborescent form, as in the liver and salivary glands,—whether they terminate by twig-like cæca, as in the liver, or in grape-like clusters of cells, as in the salivary glands, pancreas, and mammary gland,—their only connexion with the blood-vessels, in all cases, consists in the latter ramifying and forming a capillary net work on their walls and in their interstices; and thirdly, that the finest secreting tubes, namely those of the liver and kidneys, are always some few times larger in diameter than the minute ramifications of the arteries and veins.

The individual forms in which the secreting canals are arranged are various; but all secreting glands agree in this, that by the interior of their tubes,—of their convoluted or ramified canals,—they afford an extensive surface for secretion, and that the same action is performed by the inner surface of their canals or ducts, as is effected in a more simple manner by a plane secreting membrane. The end, therefore, which Nature seems to have aimed at, by the peculiar distribution of the substance destined to produce a chemical change in the organic matter, is the obtaining a great surface in a small space; and she has attained this end, as will be seen in the following anatomical detail, in the most various ways.

The simplest glands are mere recesses of greater or less size in the surface of a membrane: sometimes they are only very shallow depressions, such as the simple crypts of the mucous membranes; in other instances, they form distinct sacs with a narrow neck, such as the follicles of the mucous membranes, among which the so-called glands of Peyer must not be included; their structure will be described in the section on digestion: in other cases, again, the membrane is reflected back in the form of a tube, of which we have an example in the mucous canals under the skin of fishes. The *follicle*, "*folliculus*," and *tube*, "*tubulus*,"

* Meckel's Archiv, 1827. † Isis, 1828.

‡ J. Müller, de Gland. Struct. Penit. Lips. 1830.

may indeed be regarded as the elementary forms of the two principal modifications in the structure of glands. But even the follicles, which appear to be the most simple, have a complicated structure; either the interior of the follicle presents cellular dilatations, or the sac is clustered like the Lieberkuehn's crypts of the intestines and the Meibomian glands, or the walls of the follicle are themselves formed of cæcal tubes running perpendicularly to their surface, which is the structure of the gastric glands of birds and other animals.*

The different forms of more complicated glands resulting from the further developement of the follicle and tube by increase of the secreting surface, may be distinguished as follows. Several of the sacs or tubes are often closely associated together,—*folliculi aggregati;* sometimes in a linear manner, as the Meibomian glands; in other instances in a mass, like the glandular layer in the proventiculus of birds. In this aggregated form the openings of the separate follicles remain distinct; but nature attains the same end by assembling the follicles in one mass opening by a single orifice,—*folliculi compositi, conglomerati;* the tonsils, the labial and buccal glands, and the prostatic gland of many mammalia, have this structure; the mammary gland of the ornithorhynchus, and the pancreas of the sword-fish and thunny, are likewise instances of this form of gland.† If we imagine the same process of the developement of a compound gland to be carried still further, the separate follicles of the composite follicle will send out smaller branches, and a ramified cavity with twig-like or vesicular extremities will result. The compound follicles also may, like the simple follicles, be aggregated together, and then form a larger glandular mass with several or many efferent ducts, of which the human prostate is an example; it consists, namely, of several smaller glands aggregated together, each constituting, as it were, a ramified tube with cellular extremities. By the still further progress of the mode of complication here indicated, a compound gland is formed. But only one series of compound glands is developed in this way. A second series consists of those which are constituted of tubes which do not ramify, or only to a very inconsiderable extent: here the increase of surface is obtained by the length and convolution of simple canals which in their entire length have a nearly equal diameter.

1. *Compound glands with canals of the ramified type.*—The principal glands comprehended under this head are the lachrymal, mammary, and salivary glands, the pancreas, and the liver. They are divisible into two groups: *a.* glands in which the ducts ramify with a certain degree of regularity, the principal trunk giving off branches laterally at

* Boehm, de Gland. Intestin. Struct. Penit. Berol. 1835.—Boyd, Edin. Med. Surg. Journ. 1836, p. 382.

† J. Müller, loc. cit. Tab. 3.

certain intervals, these sending out in the same way side branches, which in their turn afford a third set; this is the mode of ramification in the lobulated glands,—the lachrymal, mammary, and salivary glands, and the pancreas; and hence it is that these glands have orders of lobules loosely connected by cellular membrane, which correspond to the degrees of division of the ducts. The smallest parts of such glands visible with the naked eye are in some instances granules, or acini, which are only aggregates of cells seated in clusters on the extremities of the most minute secreting canals, and surrounded by a network of capillaries; the cells themselves being too minute to be visible except in the distended state and with the aid of the microscope. In other instances, the minute secreting canals are arranged in the form of extremely delicate cæca around the branches of the duct, like the leaves of mosses on their stem; this form of ramification is seen in the liver of the higher crustacea, and in the lachrymal gland of tortoises and turtles, and likewise gives rise to the formation of lobules. In other glands again, as in the Cowper's glands of the hedgehog,* the radicle ducts of a minute lobule terminate as in the last described forms without becoming vesicular, but are arranged in tufts of twig-like tubes.

b. The second group of the glands with ramified secreting tubes, consists of those in which the ramification is irregular, and in which there is no division and subdivision of the gland into lobules. The liver belongs to this group; the tufts of the most minute branches of the biliary ducts form acini, it is true; but these acini are united into one lobe, or several common lobes, without being previously collected into lobules.

It is this irregular mode of ramification, and the circumstance that the final branches of the ducts terminate not in cells, but, after manifold division, in twigs of microscopic minuteness, a great number of which are united to form what is called an acinus, which characterise the liver of vertebrate animals. The liver of the invertebrata belongs to the first group.

We will now describe the structure of the principal glands of this class,—the glands with ramified secreting tubes,—which are met with in the human subject.

A. *The lachrymal gland.*—In the arrangement of the secreting canals of the lachrymal gland, two principal forms are observed: the one is that which I discovered in the chelonian reptiles; the other, that which prevails in the rest of the vertebrata, birds and mammalia. In the chelonia, the gland is formed of a number of club-shaped lobes, which are united together by means of the efferent ducts which run in their interior. The duct of each lobe is pretty uniform in diameter, and into it open an innumerable quantity of microscopic tufts of cæca, which are arranged around it at right angles to it, like the foliage of a moss on its stem.† In *birds* and *mammalia* the secreting canals of the lachrymal glands are regularly branched, and terminate in each acinus in a

* J. Müller, loc. cit. Tab. iii. fig. 8, 9.

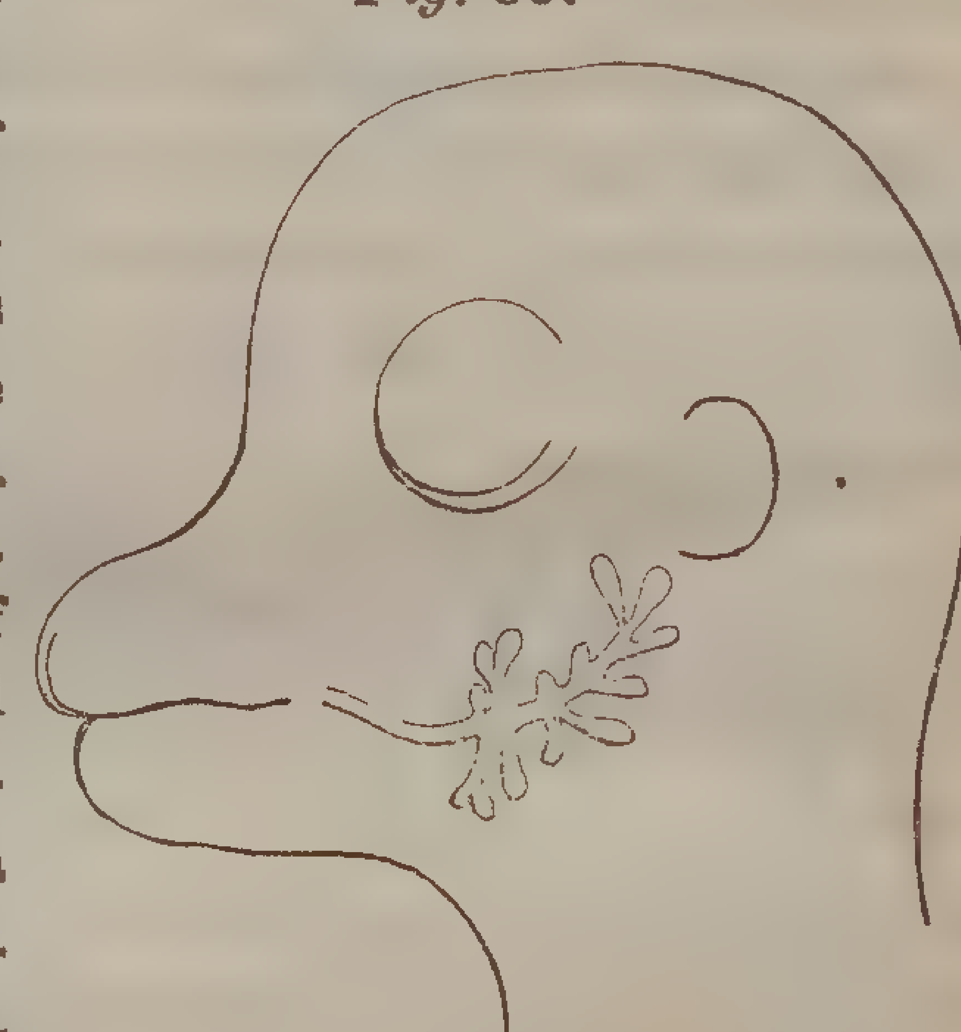
† Idem. Tab. v. fig. 4. [The microscopic measurements of the elementary parts of all the glands will be found in the table at the end of this chapter.]

number of little cells. In birds these cells are very large; and in them, and likewise in the horse, the cells can be filled with mercury from the efferent duct.

B. *Mammary gland.*—The varieties of conformation of this gland may be referred to *two general types*. It is either composed of cæca, or of branched ducts which terminate at length in bunches of microscopic cells. The first form has been examined accurately only in the *ornithorhynchus*, in which it was discovered by Meckel. The branched cæca, which open close to each other in great numbers on a plane surface, present in their interior, however, as Mr. Owen has pointed out,* a somewhat more complicated follicular structure. Von Baer † has stated, that the mammary gland of the *cetacea*, which opens by a single orifice only, also consists of cæca. But from the examination of the mammary gland of a porpoise, I am inclined to think that the cæca described by Baer were merely the larger lactiferous ducts, and that the gland is not much less complex in structure in the cetacea than in the other mammalia. The mammary gland opens on the surface of the nipple in some *mammalia*, as the ruminants, by a single orifice; in others, as man and the carnivora, by several: in the latter instances, there are, in fact, several glands in each mamma. The structure of these glands may be very beautifully shown by filling the ducts even to the terminal cellules with mercury.‡ The diameter of the cellulæ lactiferæ is from ten to thirty-five times greater than that of the smallest capillary vessels in the human body.§

C. *Salivary glands.*—The salivary glands of *insects* are, like the other glands of these animals, long cæcal tubes. In the *mollusca* I have found them of spongy and distinctly cellular structure.|| In *fishes* there are no salivary glands. In *serpents* the salivary glands, which must not be confounded with the perfectly distinct poison glands, are simple in their structure; they are seated partly on the upper and under lip, in part under the tongue, and in part, as I have discovered, near the nostrils; they have a granular aspect, and a cellular internal structure; those of the upper and lower lips consist of numerous distinct glands arranged in a linear manner, and opening by separate orifices. The poison glands have a totally different structure. They generally consist of a series of lamellæ attached to the efferent duct, each lamella being again formed of branched cæca.¶

Fig. 35.**



The structure of the sub-maxillary glands in *birds* has been examined by Professor E. H. Weber and myself, and we have found them to consist of an aggregation of several compound glands with distinct orifices; for example, in the gallinaceous birds and geese. The sublingual glands of the woodpecker, on the contrary, are larger and single. In the first kind, each separate gland, which has a granular aspect, consists of a ramified follicle, of which the walls are beset with cells; in the second kind the structure is the same, but more complicated.†† In *mammalia*, the form in which a salivary gland first appears, is, according to Weber's and my own observations, that of a simple canal with bud-like processes, (fig. 35,) lying in a gelatinous nidus or "blastema," and communicating with the cavity of the mouth. As the developement of the gland advances, the canal becomes more and

* Philos. Transact. 1832. † Meckel's Archiv. 1827, p. 559.

‡ J. Müller, loc. cit. Tab. vi. fig. 1—8. § Ibid. Tab. vi. fig. 5.

|| See the representation of the structure of the salivary gland of the murex tritonis in the work just cited. Tab. xvii. fig. 6. ¶ Ibid. Tab. vi. fig. 1.

** [First appearance of the parotid gland in the embryo of the sheep; after Müller, loc. cit.] †† Ibid. Tab. vi. fig. 6—8.

more ramified, increasing at the expense of the germinal mass or "blastema" in which it is still enclosed. (fig. 36.) The blastema soon acquires a lobulated form corresponding to that of the future gland, and is at last wholly absorbed.† Thus in the first stage of their developement the salivary ducts can be seen to constitute an independent closed system of tubes; but in the adult state also, the vesicles which terminate the ultimate microscopic branches of the ducts can be filled with mercury from the excretory duct. Professor E. H. Weber has succeeded in doing this in the human subject, and I have done it in the dog. The most minute cells, which, when filled with mercury, have a diameter about three times greater than that of the capillary blood-vessels, are united into small grape-like bunches or lobules which are from four to seven times larger than the cells themselves. The most minute pulmonary air cells are from five to sixteen times larger than the cells of the parotid gland.

Fig. 36.*

D. *Pancreas.*—The mammary gland, as we have seen, is in its simplest form, namely, in the cetacea, composed merely of cæca; and the pancreas likewise appears first in the same form, constituting the pyloric appendices of *fishes.* These pancreatic or pyloric cæca, which indeed are wholly wanting in some fishes, vary in their number and complexity. Sometimes they are single, sometimes very numerous, and in rarer instances they are ramified. In the cod and haddock they begin to be aggregated together, and to be branched. The ramification is still very simple in the polyodon folium, in which the cæca are very wide and short. In the family of the scomberoideæ the division of the cæca attains in some species a great degree of complexity; thus in the scomber thynnus four large trunks arise from the intestine, and ramify, each branch terminating at length in a tuft-like fasciculus of narrow tubular cæca.‡ In the sword-fish the structure is the same; with the exception that the cæca, instead of being long tubuli, are shorter, and of larger diameter. In the sturgeon, the tubes of the pancreas are united together so as to form a sponge-like cellular mass; § and in the sharks and rays the organ has attained the close texture which it has in the higher animals. The process of developement of the pancreas, as it is observed in *the tadpole,* is similar to that of the salivary glands in mammalia. But even in the adult state *in birds* E. H. Weber and I have succeeded in injecting it with mercury, so as to fill the cell-like extremities of its secreting canals.‖ The diameter of these cells is from six to twelve times greater than that of the capillary blood-vessels.

E. *The liver. Its various forms in the animal series.*¶—I will not here dilate upon the analogy which some physiologists trace between the Malpighian vessels of insects

* [Lobules of the parotid, with the salivary ducts, in the embryo of the sheep at a more advanced stage. Ibid.]

† Ibid. Tab. vi. fig. 12.

‡ J. Müller, loc. cit. Tab. vii. fig. 4, 5.

§ See Monro, on Fishes.

‖ J. Müller, loc. cit. Tab. xvii. fig. 3. 5.

¶ Representations of the structure of the liver in different animals will be found in the author's work on the glands, Tab. viii. ix. and x. and xi.

and the liver of higher animals; that is a point which will be discussed in the fourth chapter of the section on digestion. I may mention, however, that the biliary organs of *arachnida* have the form of clustered vesicles which open by efferent ducts into the intestinal canal. In the scorpion there are five pairs of these ducts. In the *crustacea*, particularly in the higher families of the order, the liver consists of large bunches of cæca united in digitate fasciculi, from which on each side one main efferent duct opens into the intestinal canal; this form is seen in the astacus aquaticus and pagurus striatus, while in other crustacea—the genera palæmon, penæus, and crangon, for example,—the liver is formed of vesicles united in bunches, and in the squillæ the lobules of the liver are spongy cellular masses. Rathke has shown that the liver of the astacus fluviatilis, which afterwards consists of cæca, is originally developed by the protrusion of a portion of the walls of the intestinal canal. In the *mollusca* the liver has already assumed very much the appearance which it has in the higher animals. When filled with bile, it appears at first sight to have a granular structure; but, as I have pointed out, inflation from the duct renders cells evident. In some large gasteropods, such as the murex tritonis, the cellular structure is so striking, and the cells so large, as to be visible even to the naked eye in the cut surface when the liver is divided.

The liver of mammalia is a very difficult subject of investigation, and it is only from its mode of developement that we can derive any certain conclusions as to its intimate structure. It is an extremely difficult matter to make a good injection of the minute biliary canals, while the blood-vessels may be injected in their whole extent.

Developement of the liver, and its structure in birds and mammalia. The observations of Rolando, Baer, and myself have placed it beyond a doubt that the liver in the embryo of the bird is originally developed by the protrusion, as it were, of a part of the walls of the intestinal canal, which is likewise the mode of developement of the lungs and pancreas. According to Baer,* the liver of the embryo of the bird is first visible about the middle of the third day, in the form of two conical hollow branches of the alimentary tube, which embrace the common venous stem. The cones increase in length, pushing before them ramifications of blood-vessels, while their base becomes gradually narrowed, and assumes the form of a cylindrical duct. The liver therefore is developed originally by the protrusion of the parietes of the intestine in the form of two hollow cones into the vascular layer that invests it externally. Internal ramifications are developed in the cavities of the cones, which at the same time become united at their base, more and more of the surrounding part of the intestinal parietes being taken up to form them, till at last the part that separated them is removed to a distance from the intestine; and the cavities, originally double, open by one mouth into the intestinal tube (fig. 37.) The gall-bladder is developed as a diverticulum from the hepatic duct.

Fig. 37.†

According to my observa-

* In Burdach's Physiologie, Bd. ii. p. 504.

† [1. Rudiment of the liver on the intestine of chick at the fifth day of incubation; — 1. The heart; 2. the intestine; 3. diverticulum of the intestine, in the coats of which the liver (4) is developed; 5. part of the mucous layer of the germinal membrane. After Müller, loc. cit.]

tion, the parietes of the hollow process of the intestine that afterwards forms the liver, have at first,—namely, on the fourth day,—nearly the same thickness as those of the rest of the intestine : soon, however, they become much thicker, but still enclose a cavity, which diminishes in size in proportion as the hepatic tubes become further developed ; the formation of the latter being announced by the appearance in the thickness of the hepatic substance of ramified figures and cæcal-shaped granules, which latter are not distinctly hollow. The biliferous canals therefore do not owe their developement to the continued protrusion of new parts in the same manner as the first cones were formed, but by the further organization of the portion of the intestinal membranes already protruded. Respecting the later stages of the formation and ramification of the biliary canals, we have some observations of Harvey and Malpighi. Harvey* described the substance of the liver to grow like sprouts or buds from the external surface of the blood-vessels ; on the sixth, seventh, and ninth days the liver appeared to Malpighi† to consist of cæca. I have, with the aid of the microscope, followed still further the progress of its developement. On the surface of the liver in the embryo I have seen innumerable cæca, or short twig-like bodies, of a yellowish white colour, projecting from the blood-red substance, in which they lie very closely aggregated together. In more advanced embryos the cæca appear more branched, so as to have the form of feathers, or even of arborescent tufts. One of the cæca measures about $\frac{1}{588}$ of an English inch in diameter.

I have in a few cases succeeded in injecting the biliary canals from the hepatic duct with size and vermilion, so as to make the liver quite red. The minute acini were then seen to be formed of ramified divisions of the biliary ducts, which rise in fasciculi, constituting the acini, to the surface, spread out and divide still further, but without diminishing in size. It requires patient microscopic examination of the injected liver to recognise the most minute branches of the ducts, and they lie so close together that they appear to be united one with another : their diameter varies from $\frac{1}{855}$ to $\frac{1}{789}$ of an English inch ; they are larger therefore than the capillary blood-vessels. It is remarkable that the minute biliary canals of the embryo, unlike the minute canals of the salivary glands, terminate, as we have seen, by blind twig-like extremities, and that no bud-like or vesicular enlargements appear on them at a later period of their developement. Krause,‡ however, has seen the extremities of the biliary canals assume a vesicular form when he forced air into the ducts, and he concludes that the acini of the liver, like those of the salivary glands, are formed of bunches of vesicles, in which the ducts terminate. The diameter of the cells he states to be from $\frac{1}{42}$ to $\frac{1}{37}$ of an English line.

It sometimes happens that the liver, being macerated in bad spirit, separates into its acini. Thus, in the anatomical museum at Berlin there is the liver of a polar bear which has by maceration become separated into its acini.§ The smaller divisions of the ducts are no longer detectible; they may perhaps be contained in the interior of the bunches of the acini, which are connected in a ramified form with the divisions of the hepatic vein, a small twig of the vein being sent into each of the branches of hepatic substance. Each of the solid branch-like portions of hepatic substance which enclose the small twigs of the hepatic vein, and are themselves only one-fourth of a

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* Exercit. de generat. animal. 19.

† De format. pulli, 61.

‡ Mueller's Archiv. 1837.

§ It must be remarked that these observations on the structure of the liver of the polar bear were made subsequently to the discoveries of Mr. Kiernan, which are detailed in the next page. [This note is added by Prof. Müller in the present edition of the original.]

line in diameter, ramify still further without diminishing in size, and at their termination are indeed enlarged, forming bodies of which the diameter is half a line, and the length two or three lines, and from which here and there short processes project. The delicate biliary canals can no longer be detected in their substance. It is remarkable that the veins, which are thus invested by the substance of the liver, like the branches of mosses by their leaves, are not divisions of the vena portæ, but of the hepatic veins. In the preparation of which I am speaking it may be seen, at those parts where the substance of the organ is still held together by cellular tissue, that the ends of the ramified bodies which are connected with the hepatic veins are identical with the parts on the surface of the liver which are termed acini. The ramified cylinders here described must therefore themselves be composed of aggregations of the much more minute biliary tubes which we have described as seen after injection, and as demonstrated by observations on the mode of developement of the organ.

Several writers, Autenrieth, Bichat, Cloquet, Mappes, and Meckel, have spoken of two substances as existing in all parts of the liver, and as constituting a cortical and medullary portion of each acinus. From my researches, however, it results that there is but one kind of real hepatic substance, formed of agglomerated biliary canals; but the ramified divisions of this substance being connected by a vascular cellular tissue, which is often of a dark colour, a contrast between this and the yellow substance of the acini is produced. A similar relation of the constituent parts of the liver exists in the embryo of the bird,—in it the yellowish twig-like ramifications of the biliary canals are seen on the surface of the organ rising out of a reddish vascular tissue.

Distribution of the blood-vessels in the liver.—It is known that injection thrown either into the hepatic artery or into the portal vein fills the same capillary network, from which, on the other hand, the hepatic veins likewise arise. It appears, therefore, that the arterial blood of the hepatic artery, and the venous blood of the porta, become mixed in the minute vessels of the liver, and that the secretion of bile probably takes place from both. The most delicate capillaries are, as I have said, more minute than the microscopic cæca of the biliary ducts. They form a network which occupies all the interstices of, and invests, the secreting canals, with which, however, they do not immediately communicate; for in the embryo of the bird, and in the larvæ of the frog also, the secreting canals of the liver can be seen with the aid of the microscope to terminate on the surface of the organ with blind extremities. In the larva of the salamander, the blood can with the microscope be seen circulating between the acini of the liver.

The very valuable researches of Mr. Kiernan * have advanced our knowledge of the anatomy of the liver. He describes the lobules of the liver (which by other anatomists are termed acini) as leaf-shaped, but not flattened, bodies, which send out several short rounded processes: his description of their form is indeed similar to that which we have given above of the acini of the macerated liver of the polar bear. In the interior of each lobule runs a central vein (venula intralobularis), which is a branch of the hepatic vein, and which returns the blood from the capillary network of the lobule. The branches of the hepatic vein from which these intralobular veins arise, run in canals formed by the bases of the lobules, and on their inner surface appear perforated by foramina which are the mouths of the venulæ intralobulares issuing from the bases of the lobules. All the lobules of the liver therefore contribute by their bases to form canals for the hepatic veins. The external surface of each lobule is invested by a sheath of cellular membrane,—a prolongation of the capsule of Glisson,—and in this cellular membrane, which at the same time separates the lobules one from another, the

* Philosoph. Transact. 1833, pt. ii. p. 711.

branches of the hepatic artery and those of the portal vein run. The latter veins (the venæ interlobulares) terminate in the capillary network of the lobule, from which the intralobular veins on the other hand arise. Congestion of either of these systems of veins gives rise to a difference of tint in the corresponding part of each lobule, of which the natural colour is yellowish : if the portal or interlobular veins are congested, the centre of the lobule appears pale ; if the congestion affects the hepatic or intralobular veins, it is the margin of the lobule which is left of the paler yellow colour ; and hence has arisen the erroneous supposition that the lobules are composed of two substances.

The cellular tissue of the capsule of Glisson is continued from the transverse fissure into the interior of the liver, forming a common sheath for the hepatic artery, portal vein, and hepatic duct ; surrounds all the branches of the porta and the accompanying branches of the artery and duct, and terminates at last in the interlobular cellular tissue. The branches of the hepatic vein are in no way connected with these cellular sheaths.

The hepatic artery is, according to Kiernan, distributed principally to the walls of the gall-bladder, the bile-ducts, and the other blood-vessels, to which it supplies the vasa vasorum. From the capillary network that results from its ramification, he supposes the blood to pass into branches of the portal vein, and from thence into the hepatic veins ; for, when fine injection was thrown into the hepatic artery, the portal veins became filled, but not the hepatic veins. Having injected the porta first with blue, and the artery afterwards with red, he found branches of both vessels in the coats of the vessels, of the bile-ducts and of the gall-bladder ; the lobules of the liver were coloured blue, and merely points of the red injection were seen here and there in their marginal portion. These are Kiernan's grounds for believing that those branches of the hepatic artery which enter the lobules do not terminate directly in the hepatic veins, but pour their blood first into branches of the porta, from which it is afterwards transmitted to the hepatic veins. The commonly received opinion that all the blood of the liver — that of the hepatic artery as well as that of the portal vein—is poured into one and the same capillary system, would, according to Kiernan's view, be incorrect ; but his opinion is not yet satisfactorily confirmed, and it is opposed to what we can observe in the injected preparations of Lieberkühn, in which the injected matter is seen to have frequently passed into the same network as readily from the one as from the other vessel.

Kiernan gives the following description of the mode of termination of the biliary ducts. The minute divisions of the ducts which lie between the lobules divide and subdivide into numerous branches, which at last anastomose with each other, he says, and form a plexus which is independent of that of the blood-vessels, and constitutes the proper substance of the lobule.* I have not been able to satisfy myself of the existence of anastomoses between the biliary ducts in the instances in which I have injected them ; the minute canals appeared to me to terminate in short panicle-like tufts which lay closely interwoven together : the history of the developement of the organ is likewise opposed to the belief of the existence of such anastomoses ; for in the embryo of the fowl, and the larva of the frog, twig-like terminations of the ducts are distinctly visible by the aid of the microscope on the surface of the liver. Kiernan explains the appearances here described as belonging to the fœtal liver in a different way ; he supposes the yellow lines to be the interstices between the radiations of the veins, and not ducts. But this excellent inquirer would not have advanced such an opinion if he had himself examined with the microscope the biliary canals in the embryo of the bird, and in the larva of the frog. After repeated examination with the microscope, no doubt exists in

* Phil. Transact. 1833, pt. ii. Tab. xxiii. fig. 3.

my mind as to the mode of termination of the ducts in the embryo: whether in the adult the acini likewise consist of aggregated bodies which do not anastomose, or of a plexus of ducts, as Kiernan maintains, is not yet determined; and it is difficult to decide the question, for the minute biliary canals of the lobules, when well injected, being so interwoven and closely aggregated together, may have the appearance of a plexus without such plexus really existing, and in some instances even a plexus of veins or capillaries filled by extravasation may be mistaken for anastomosing biliary canals.

2. *Glands with a tubular structure.* — The kidneys and testicles are examples of this structure in the human body. The increase of secreting surface is here obtained by means of convoluted canals of great length, which do not ramify, or only in a slight degree, and maintain the same diameter in the greater part of their course.

F. *The kidneys.**—The kidneys of the lower vertebrata,—the fishes, amphibia, and reptiles,—present no marked division into medullary and cortical portions. The texture of the kidneys of *fishes* is constituted wholly of convoluted tubes (ductus uriniferi), which, taking their rise from the ureter, preserve the same diameter throughout, and most probably terminate by cæcal extremities.

In the kidneys of *frogs* the tubuli uriniferi are directed from one border of the kidney to the other, like the barbs on the shaft of a feather; are in part straight, in part convoluted, and terminate by blind extremities. In *serpents* the kidneys consist of a series of lobes, along the external border of which the ureter descends, and sends a branch into the concavity of each lobe. The branch, as soon as it has entered the lobe, divides into a tuft of small tubes, which become continuous with the excessively convoluted tubuli uriniferi that form the proper substance of the kidneys, and appear to terminate by slightly dilated cæcal extremities. The canals in the kidneys of *chelonian reptiles* resemble exactly in their distribution those of the kidneys of birds.†

The kidneys of *birds*, which consist of several distinct lobes connected only by the branches of the ureter, present an approximation to the structure of the analogous organs in mammalia, inasmuch as their tubuli uriniferi are collected into pyramidal masses, of which the apices or mammellæ are received each into a branch of the excretory duct. On the surface of the kidneys small convolutions are seen like those on the surface of the brain, or like those formed by the approximated margins of some much curled or undulated leaves. These convolutions are formed by the laminæ into which the urinary canals arrange themselves as they rise to the surface, and in which the individual canals run parallel to each other from within outwards. The arrangement of the laminæ may be best conceived by gathering one side of a handkerchief together, while the opposite border is allowed to fall into folds like those of a curtain or frill. This peculiar structure is most evident in the embryo, where the folds of the laminæ are indeed very similar to those of a ruff or frill. In the old bird the ducts can by the aid of atmospheric pressure be injected with size and vermilion, and then the disposition of the ends of the urinary canals on the surface of the kidney presents a beautiful appearance; each tubule gives off branches laterally in a pinnate form, like a feather, or like the branching of a stag's antler. The above description of the disposition of the urinary canals in the

* Representations of the structure of the kidneys in different animals will be found in the author's work already cited, Tab. xii. xiii. and xiv.

† On the afferent veins of the kidneys in amphibia and reptiles, see page 169.

kidneys of the bird is founded on the observations of Huschke and myself. I have perceived in the beautiful injected preparations of Professor Retzius in Stockholm that the lateral branches of the pinnate ducts are continued still further, sinking into the substance of the kidney, without, however, giving off any branches; after diminishing gradually, but only very slightly in size, they appeared to form loops, but I could not ascertain distinctly their mode of termination.*

In *the embryo of mammalia and of the human subject* the kidney consists of several distinct lobes (renculi) which are connected only by the divisions of the pelvis of the kidney. The renculi correspond in number to the pyramidal or medullary portions of the kidney of the adult animal. In several animals,—the bear, the otter, and the cetacea,—the renculi remain separate throughout life. Each renculus in the animals just mentioned, as well as in the fœtus of mammalia and of man, consists of the pyramidal medullary portion, with a layer of cortical substance investing its base like a cap, and continued at its sides even as far as the mammella. After the union of the renculi, therefore, the pyramidal bodies are necessarily separated from each other by cortical substance, which extends between them towards the papillæ or mammellæ. In the medullary portions the urinary canals run, as is well known, in straight lines from the base of each pyramid towards the mammella, two occasionally uniting to form one tube. In their course from the base of the pyramid to the mammella they undergo in the horse a trifling increase of size; while in the human subject, according to Weber, not the slightest enlargement of their diameter takes place. At the base of each pyramidal mass the bundles of tubuli uriniferi that compose it separate, and the tubes become distributed in all directions in the cortical substance. The fasciculi of urinary canals (the pyramids of Ferrein) which compose the larger pyramidal bodies of Malpighi extend but a short distance into the cortical substance; the outer canals of each fasciculus being the first to leave it, and the others in their order, till the fasciculus is wholly resolved into its separate canals. The entire cortical substance consists of convoluted ducts, of which the diameter remains the same in their whole length. In the horse's kidney the cortical substance is thin, and the convoluted tubes therefore less numerous. It is very difficult to find the extremity of the convoluted urinary tubules. In the kidney of the squirrel the canals appeared to me to divide towards their extremity into several cæca, the ends of which were not at all or only very slightly dilated. Weber examined the human kidney with the microscope, but could find no ducts terminating with free ends; all seemed to form loops. By the aid of the air-pump I have succeeded in injecting the horse's kidney from the ureter, and have discovered that in it the tubuli uriniferi anastomose freely. According to Krause, the urinary canals both anastomose with each other, and also terminate by free cæcal extremities, just as is the case with the convoluted tubuli seminiferi. To inject the canals in the cortical portion of the kidney, it is necessary to expose the surface of the organ to the vacuum of an air-pump; the pressure of the atmosphere then forces the injection through the ureter into the tubuli uriniferi as far as the surface of the kidney. Huschke was the first to use this method of injection in the case of the kidneys; it does not succeed very well except in the horse.

The *disposition of the blood-vessels in the substance of the kidney* is extremely interesting. In the cortical structure they form the ordinary capillary network, of which the meshes are so close that the intervals are not many times larger than the diameter of the capillaries that enclose them. Among the tubuli uriniferi of the cortical substance lie the acini of Malpighi, which are larger than the urinary canals, (see the table of measurements,) and are visible even with the naked eye. Schumlansky has

* On the structure of the kidney in birds, compare the remarks of Huschke in the Isis, 1828, page 565.

drawn them much too small. They lie in vesicular cavities of the cellular tissue between the tubuli uriniferi, and consist wholly of convoluted blood-vessels. It is remarkable that they exist in the kidneys of most, perhaps of all, vertebrate animals; they have been found in the kidney of the frog, toad, salamander, turtle, and tortoise, birds, mammalia, and man. Schumlansky first advanced the hypothesis that these *glomeruli* are the source of the urinary secretion,—that the tubuli uriniferi take their rise in them. The more accurate examinations of Huschke and myself have shown that such is not the case, for the glomeruli or corpora Malpighiana can be injected only from the arteries, never from the secreting canals. In the salamander, too, Huschke has seen the blood-vessel, which enters each of the glomeruli, issue from it again, after having made numerous convolutions.* They can be filled with injection from the arteries as easily as from the veins, and are simply receptacles for blood.

The convoluted tubuli uriniferi themselves are the seat of the secretion of urine, which is poured out by their whole internal surface, not by their extremities only. They are everywhere surrounded by minute currents of blood, circulating in the capillary network which fills their interstices, and is extended over their external surface. The fluid part of the blood may permeate the delicate parietes of the uriniferous canals, and suffer in its transit a chemical change; or the effete matters contained in the blood of the capillaries may be attracted and separated from it by the agency of the secreting canals.

In the medullary portions of the kidney the blood-vessels run between the urinary canals in straight lines from the cortical portion towards the mammella. These straight blood-vessels are easily injected either from the arteries or the veins, and were formerly supposed to be urinary canals, and to prove the existence of a communication between the blood-vessels and ducts of glands. But they differ from the secreting canals in becoming smaller as they approach the mammella, on which they terminate in the common capillary network which surrounds the openings of the tubuli uriniferi.

The secreting canals of the kidneys are extremely similar to the tubuli seminiferi; both are convoluted and form anastomoses, but the canals of the kidneys are the more minute: in the human subject they are several times smaller than the seminal tubes, therefore cannot be seen with the naked eye; and, by their close aggregation, give to the cortical portion of the kidney the appearance of a solid mass. In serpents, and in the sharks and rays, on the contrary, they are so large as to be visible without the aid of a glass.

G. *Testes.*†—In *insects* the forms presented by the testes are infinitely various. The fundamental character of all is, however, that a large secreting surface is obtained in a small space, and all the varieties of form by which this end can be realized are here displayed.‡ We meet with insects in which the testes are simple, undivided, more or less, convoluted tubes, or tubes interwoven into plexuses; while in other instances the tubes end in ramifications with vesicular extremities, or in whorls, or radiated aggregations of cæca. Sometimes the testis is composed of a mass of cæca united in a brush-like form, or in that of a horse's tail; in other instances, namely in the scorpion, as I have discovered, the tubes anastomose, forming loops. In all these forms of testes the fluid is of course secreted only on the inner surface of these tubes, cæca and vesicles; and nature attains the same end by means of a simple but much

* Tiedemann's Zeitschrift für Physiol. iv. Tab. vi. fig. 8.

† The different forms of the testes in the animal kingdom are represented in Table xv. of the author's work on the glands.

‡ See Leon Dufour, Ann. des Sc. Nat. tom. vi.—Succow, in Heusinger's Zeitschr. für organ. Physik. tom. ii.

elongated canal, as by shorter branched tubes, or numerous aggregated cæca. Among the *mollusca*, likewise, the testes have very various forms; but in most instances they are constituted either of grape-like bunches of vesicles, or of cæca united together in tufts.

In *fishes* there are two modifications in the form of the testes: they either consist of ramified tubes, which is generally the case; or they are composed of granules. When the testis has the granular form, there is no vas deferens. The semen is formed in the interior of the granules, which bursting, the fluid is most probably effused, like the ova of some fishes, into the abdominal cavity, from which it escapes by openings leading directly to the exterior,—openings, which exist only where the testes have this form, namely, in the eel and lesser lamprey according to Rathke, and, according to my own observation, in the sharks and rays. In the eel and lesser lamprey there is but one abdominal opening, in the sharks and rays there are two. The organ which in these latter fishes has been called epididymis and vas deferens has no connexion with the testes, and is a peculiar gland.*

The testes of the amphibia consist of short blind tubes; they have no epididymis; the vasa efferentia unite immediately to form the vas deferens. The epididymis first appears in *reptiles*, being formed by the convolutions of the vasa efferentia and vas deferens.

The structure of *the human testis* has been recently investigated by Sir A. Cooper,† and with still greater success by Prof. A. Lauth,‡ and by Krause.§ Sir A. Cooper describes the lobules of the testis as being not merely separated from each other by processes of the tunica albuginea which form septa between them, but as being each enclosed in an exceedingly delicate membrane. The tubuli seminiferi taken together are all directed towards the rete testis, and may be regarded as forming one cone of which the apex is towards that part; each tubulus, likewise, is so disposed, that, by the convolutions into which it is reflected, becoming smaller and smaller as it approaches the rete, it forms a cone the apex of which is directed to the same point. The diameter of all the tubuli is the same. [The measurements are given in the table at the end of the chapter.] A lobule contains, according to Lauth, sometimes one, sometimes two, at other times several tubuli. He reckons the number of the tubuli at 840, and the length of one at two feet three inches. Krause found from 404 to 484 lobuli in a single testis. I had observed some of the seminal tubes terminating by free extremities in mammiferous animals; the observation is most easily made in rodentia on account of the larger size of the tubuli in them. Lauth has but once seen a seminal canal ending with a free extremity in the human testis. Krause has seen such free ends of the tubuli seminiferi frequently, and confirms the opinion of their terminating in that way as well as by anastomosis. Lauth attributes the circumstance of free extremities of the tubes being so seldom seen to their uniting with each other so as to form loops. He describes the division and re-union of the tubes to be so frequent that, in a small portion which he spread out, and in which there were about forty-nine inches of tube, he found about fifteen anastomoses. It is, however, only towards their extremity that the seminal tubes anastomose thus freely. The discovery of the anastomoses of the seminal tubes is perfectly original.

The tubuli seminiferi form a system of closed tubes of the same diameter throughout, hence we cannot suppose that the semen is secreted merely by their extremities; on the contrary, their whole internal surface must perform that office; and, since

* See J. Müller, in Tiedemann's Zeitschrift für Physiol. iv.

† On the Structure of the Testis, translated into German. Weimar, 1832.

‡ Mém. de la Société de l'Histoire Natur. de Strasbourg, liv. ii.

§ Müller's Archiv. 1837. 20.

they are fifteen times thicker than the smallest branches of the arteries which ramify on their coats, a direct inosculation between them cannot be thought of.

When the tubuli seminiferi have reached to within a line or two of the rete testis, they cease to be convoluted: several unite together, and then enter the rete under the name of the tubuli recti, of which there are, according to Lauth, certainly more than twenty, which Haller supposed to be their number. Their diameter is greater than that of the tubuli seminiferi. The rete testis occupies a great portion of the upper border of the organ; it commences a short distance from the internal extremity, and extends as far as the external third of the upper border, varying in length from six to eleven lines; it is contained in the thickness of the tunica albuginea, and gives rise to an internal white process of the albuginea, called the corpus Highmori, the height of which measures from two to four lines, its base from three to six lines. The rete testis consists of from seven to thirteen vessels, which run in a waving course, anastomose with each other, and again divide, being all connected together. The vasa efferentia, which issue from the rete and go to form the head of the epididymis, are at first straight, but soon become convoluted, each forming a cone of which the apex corresponds to the rete testis, the base to the head of the epididymis. Lauth says that the efferent canals diminish in size as they approach the epididymis; their number is from nine to thirty, their length eight inches. They enter the canal of the epididymis one after another, the interval between the entrance of every two being, according to Lauth, three inches three lines. The average length of the canal which forms the epididymis is stated by Lauth to be twenty-one feet.

The vasculum aberrans is usually found at the angle which the vas deferens makes when it applies itself to the epididymis; it generally unites with the termination of the canal of the epididymis, less frequently with the commencement of the vas deferens. In rare cases there are several vasa aberrantia. The vas aberrans is a cæcal appendage of a yellowish colour; its length, when unravelled, varies from one and a half to fourteen inches. The part nearest to the epididymis is always smaller than the rest of the canal, and much smaller than the tube of which the epididymis is formed. Towards its cæcal extremity it becomes gradually larger; and sometimes, after being dilated for a certain extent, terminates by becoming again extremely minute. Its office is evidently the secretion of a fluid which it pours into the epididymis. Whether it bears any relation to the corpora Wolffiana of the embryo is not known.

The *general results relative to the structure of the glands*, which may be deduced from the foregoing anatomical description of the individual secreting organs, are the following:

1. However various the form of their elementary parts, all secreting glands without exception (not only those of the human body, but all met with in the animal kingdom) follow the same law of conformation, and constitute an uninterrupted series from the simplest follicle to the most complex gland.

2. No line of demarcation can be drawn between the secreting organs of invertebrata and those of vertebrate animals; not merely do we meet with the simplest sacs and tubular secreting organs, like those of insects, in the higher animals, but there is a gradual transition from these simple secreting organs of insects to the glands of the most perfect vertebrata. The mammary glands of the ornithorhynchus, the simplest salivary glands of birds, the prostate gland of many mammalia, the

pancreas of most fishes, are as simple as the secreting organs of the crustacea.

3. All glands agree in affording by their interior a large surface for secretion. The varieties of internal surface by which the great end,—extent of surface in a small space,—is attained, are very numerous. Nature displays here, as elsewhere, an infinite profusion in the variation of forms, without departing from the simplest laws of developement. An extraordinary variety of form is presented, with almost a vegetable character, by the seminiferous tubes in insects; and still more extraordinary is the variety in the form of the secreting canals which attends the increasing complication of the more perfect glands in the higher animals; but all glands have the common character of being an efflorescence, as it were, from the principal efferent duct in the form of cavities or canals with closed extremities. Malpighi's theory of the structure of glands is therefore certainly correct, its truth has been placed beyond doubt by recent researches: but Malpighi was not acquainted with the true glandular elements; the parts in the compound glands which he called follicles are not really the elementary parts, but are themselves formed of much more minute elements agglomerated together around the branches of the efferent ducts. Moreover, the blind extremities of the secreting tubes are not always follicles; they may be long cæca, or ramifying cæcal canals united in a pinnate form; sometimes they are bunches of cells, in other instances large convoluted tubes which preserve their diameter throughout, and anastomose frequently with each other. The main point in Malpighi's doctrine, however, is correct; namely, that all the terminal branches of the ducts have closed extremities.*

* The fact of the ducts terminating by closed extremities had been shown by Mascagni and Cruikshank with respect to the human mammary gland by injection with mercury, and by the same means with regard to the salivary glands of man and of birds, and the pancreas of the latter animals by E. H. Weber; in the kidneys of the lower vertebrata by Rathke, and in those of the higher vertebrate animals by Huschke. We have demonstrated the constancy of the same structure through all the different forms of glands from the simple cutaneous follicles to the more complex glands; in the intestinal glands, in the excreting glands, in the prostate and Cowper's glands, which consist either of cæca, or of cæcal tubuli, or of vesicles. We have inflated the lobules of the mammary gland of the rabbit from the lactiferous ducts so as to fill even the vesicular extremities of the ducts; in the hedgehog and dog we have filled the same parts with mercury, as Mascagni and Cruikshank had done in the human subject. We have filled with mercury the secreting canals and their vesicular extremities in the lachrymal gland of the goose, and have demonstrated the tuft-like fasciculi of canals in the lachrymal gland of the great turtle, testudo mydas.

We pointed out the cellular structure of the salivary glands of the murex tritonis; the fact of the secreting canals in the poison glands of serpents terminating by closed extremities, and the cellular structure of their salivary glands. We have watched the progressive developement of the secreting canals in the salivary glands of the embryo

4. *Acini*, in the hypothetical sense in which the term has been used by writers,—in the sense, namely, of secreting granules,— do not really exist; there are no glomeruli of blood-vessels with ducts arising from them in a mysterious way, as has been supposed, whatever notions may have been held regarding them.

5. The parts described as *acini* are merely masses formed by the agglomeration of the extremities of the secreting canals; frequently, indeed, they are formed of minute vesicles aggregated together in grape-like bunches, which may be injected with mercury, and are often susceptible of inflation. The only example of glands really consisting of solid granules is afforded by the testes of some few fishes, in which cases the organ has no excretory duct; the granules burst into the abdominal cavity, and are evacuated from it by an external opening.

6. In many glands which have been incorrectly described to have acini or secreting granules, there are not even the hollow vesicular acini: the secreting tubes, instead of terminating in vesicles or cells, form long convoluted canals of the same diameter throughout, as in the kidney and testes, and many other glands; or straight tubuli, as in the lachrymal gland of the testudo mydas; or short cæca, as in the liver of crustacea and the prostatic gland of many mammalia. In certain glands of a grape-like structure, such as the salivary glands, the pancreas, the mammary gland of most mammalia, the lachrymal gland of birds and mammalia, the Harderian gland, the liver of mollusca, &c. there are certainly vesicular terminations of the secreting canals constituting a "substantia acinosa." The expressions "substantia acinosa," "acini," and similar terms, are applicable consequently to such glands, inasmuch

of mammalia, and detected in all the closed vesicular extremities of the canals. Weber has filled the cells of the parotid gland in the human subject with mercury, and I have done the same in the dog. We have demonstrated the transition of the pancreatic cæca of fishes through a series of intermediate steps to the cellular pancreas. In the embryos of amphibia, birds, and mammalia, the free cæcal extremities of the ductuli pancreatici are still visible; and in the goose, the cellular extremities of the ducts, and indeed the whole pancreas, may be injected with mercury.

The liver of the crustacea consists, for the most part, of cæca or cells. We have shown that the grape-like spongy liver of the mollusca may be inflated like a lung even to its terminal vesicles and cells. We confirmed the statement of Harvey and Malpighi, that the ends of the biliary canals can be seen in the embryo in the form of microscopic twigs terminated abruptly by closed extremities.

The observations of Huschke and myself have demonstrated the existence of the urinary secreting canals as an independent system of tubes in all the vertebrata. We have observed them in fishes, salamanders, frogs, serpents, birds, and mammalia. In the last two classes we have injected the tubuli uriniferi. The similar structure of the testes—their independent system of secreting canals—has been long known; and the lungs, lastly, with their terminal cellules, are the prototype of a whole series of glandular organs.

as "acinus," according to its derivation, means a small grape. But this meaning has been gradually corrupted, through the succession of hypotheses, to that of a secreting granule, granular substance; and, since the term "acinus" is strictly applicable only in the case of a few glands, it is advisable to be very cautious in the use of a word with which so many false explanations and hypotheses are connected.

7. It has been demonstrated in the case of all glands that the blood-vessels are not continuous with the secreting tubes—that the minute vessels bear the same relation to the coats of the hollow secreting canals, and their closed extremities, as to any other delicate secreting membrane, such as, for example, the mucous membrane of the pulmonary air cells. They do not open by free mouths into the radicle extremities of the secreting canals and cavities of the glands; the arteries terminate by numerous anastomoses with the veins, forming a network which is distributed over the surface of the elementary parts of the gland.

8. Thus the blood-vessels, like the secreting canals, constitute an independent closed system of vessels; the arteries and veins, after ramifying in an arborescent manner, being connected together by a network of closed tubes.

9. It was formerly asserted that in some glands a communication exists between the ducts and the lymphatics. Such is not the case: my reasons for denying it have been already stated at page 271.

10. The system of secreting canals with closed hollow extremities is to be regarded as an efflorescence of the efferent ducts, and may indeed be observed to be developed in the embryo from an originally undivided tube.

11. The arborescent ramifications of the blood-vessels accompany the ducts in their developement, and the reticulated capillaries in which the blood-vessels terminate are extended over all the closed elementary parts of the gland and supply them with blood. In the chick we may observe the simultaneous developement of the two systems; in proportion as the developement of internal surface from a plane membrane to cæcum and ramified cæca proceeds, the vascular layer of the originally simple membrane is raised on the exterior of the efflorescence.

12. The ramified canals and tubes, which, when the structure is simple, as in insects and crustacea, and even in some glands of the mammalia, lie free and unconnected, become more aggregated together, and acquire a common covering, in proportion as their evolution is carried farther; and thus is produced a parenchyma, or solid organ. This process of developement has been made an object of direct observation in the embryo.

13. The capillary blood-vessels are for the most part much more minute than the smallest branches of the ducts or secreting canals, and

their cæcal extremities, even in the most complex glandular organs. The elementary parts of glands, though minute, are of such a size that the capillary blood-vessels form around them a network which invests them. (See the foregoing anatomical description of the different glands, and the table of microscopic measurements at the end of the present chapter). During the developement of all the compound glands, while the secreting canals are still free, not aggregated together, the same relation as to size can be seen to exist between them and the capillary blood-vessels.

14. The formation of the glands in the embryo displays the same progressive evolution from the simple to the complex state, as is observed in ascending the animal scale. The most perfect and complex glands of the higher animals, when they first appear in the embryo of these animals, consist merely of the free efferent ducts without any branches (fig. 35), and in that state exactly resemble the secreting organs of the lower animals; the glands are formed from the unbranched tubes by a kind of efflorescence or ramification.

15. The mode in which the extent of internal secreting surface of a gland is realized is very various; and no one kind of conformation is peculiar to any one gland. Perfectly different glands may have a similar elementary structure, as is the case, for instance, with the testes and the cortical structure of the kidneys. And similar glands have often a perfectly different structure in different animals; of which the lachrymal glands, examined in the chelonia, birds, and mammalia, afford an example. How various, too, is the elementary structure of the liver in the animal series; in one case being represented by simple cæca; in another, by tufts of cæca; in others again by bunches of cells, by a spongy mass; or, lastly, by branched ducts ending in feather-like terminal twigs! How infinitely various is the conformation of the secreting tubes of the testes! The kidneys alone maintain one constant character in all classes of animals; namely, that of consisting of long tubes which do not ramify, but run either parallel with each other or interwoven, although the arrangement of these tubes is subject to the greatest variation.

16. We do not observe a gradually progressive developement of the glands from the lowest to the most perfect animals; on the contrary, we meet in every class with rudimentary glands of extremely simple structure, constituting their first form in the class: thus, the salivary glands have this simple structure in birds and serpents; and the mammary gland of the ornithorhynchus, the prostate gland of rodentia, the pancreas of fishes, and the liver of the lower animals, consist merely of cæca.

17. However different the secretions of the glands may be, the substance of their elementary parts is in all instances white, or of a greyish or yellowish-white colour. There is no essential correspondence between the substance of the gland and the matter which it secretes.

Table of measurements of different microscopic parts.

	In fractions of an English inch.
Capillaries, (according to Prof. E. H. Weber)	$\frac{1}{3700}$ to $\frac{1}{1900}$
Do. in the kidneys (according to my measurement)	$\frac{1}{2490}$ to $\frac{1}{1590}$
Do. in the human iris	$\frac{1}{2490}$ to $\frac{1}{1964}$
Do. in the ciliary processes	$\frac{1}{1740}$
The smallest *pulmonary air-cells* in the human subject (according to Weber)	$\frac{1}{199}$ to $\frac{1}{69}$
Cylindrical cæca in the lung of the embryo of the bird	$\frac{1}{194}$
The *elementary vesicles* of the *mammary gland* in the hedge-hog giving suck	$\frac{1}{129}$ to $\frac{1}{99}$
Do. Do. in the dog, filled with mercury	$\frac{1}{355}$
Cells of the salivary glands in the goose, injected by myself	$\frac{1}{355}$
Do. Do. the parotid, in the new-born infant, injected by Weber	$\frac{1}{1125}$
Do. Do. Do. in the dog, injected by myself	$\frac{1}{493}$
Cells of the *lachrymal gland* of the goose, measured from my injections	$\frac{1}{310}$
Elementary parts of the lachrymal gland of the testudo mydas	$\frac{1}{475}$
Cells of the *Harderian gland* of the hare, from my injections	$\frac{1}{118}$
Do. Do. of the goose, filled with mercury, $\frac{1}{5}$ $\frac{1}{4}$ $\frac{1}{3}$ of a line.	
Cells of the *pancreas* of the goose, filled with mercury	$\frac{1}{673}$ to $\frac{1}{386}$
Elementary vesicles of the *liver* of the helix pomatia	$\frac{1}{163}$
Elementary tubes of the liver of the embryo of a jay, one inch in length	$\frac{1}{544}$
Terminal twigs of the biliary ducts on the surface of the liver of the embryo of the rabbit, injected	$\frac{1}{854}$ to $\frac{1}{791}$
Cæca of the *Wolffian bodies* of the embryo of a bird	$\frac{1}{244}$
Do. Do. of another embryo	$\frac{1}{307}$
Tubuli uriniferi of the petromyzon marinus	$\frac{1}{284}$
,, ,, of the electric ray	$\frac{1}{194}$
,, ,, of serpents, filled with mercury	$\frac{1}{388}$
,, ,, Do. their extremities	$\frac{1}{218}$
,, ,, of the owl, injected from the ureter, their extremities	$\frac{1}{543}$
,, ,, of the cortical substance of the kidney of the squirrel	$\frac{1}{619}$
,, ,, on the surface of the horse's kidney, injected from the ureter	$\frac{1}{673}$ to $\frac{1}{495}$
,, ,, in the pyramidal portions of the horse's kidney at the mammellæ, the largest	$\frac{1}{76}$
,, ,, Do. those of the medium size	$\frac{1}{188}$
,, ,, Do. the smallest seen in sections of the cortical substance	$\frac{1}{659}$ to $\frac{1}{492}$
,, ,, in the cortical substance of the human kidney (Weber)	$\frac{1}{512}$
,, ,, in the pyramidal portions	$\frac{1}{577}$
,, ,, measured on the mammellæ	$\frac{1}{923}$
The *glomeruli or corpora Malpighiana* of the human kidney	$\frac{1}{131}$
The same (Weber)	$\frac{1}{138}$ to $\frac{1}{104}$
The straight arteries in the pyramidal portions of the dog's kidney	$\frac{1}{1223}$ to $\frac{1}{542}$
The same near the mammella, where they form a network	$\frac{1}{2197}$
Tubuli seminiferi of a young cock	$\frac{1}{174}$
,, ,, of a squirrel	$\frac{1}{63}$
, ,, of the hedge-hog	$\frac{1}{95}$
,, ,, of the human testis	$\frac{1}{195}$
,, ,, ,, ,, filled with mercury	$\frac{1}{97}$

	In fractions of an English inch.
The tubuli seminiferi of the human testis, according to Lauth	$\frac{1}{170}$
" " " filled with mercury	$\frac{1}{132}$
The tubuli recti (Lauth)	$\frac{1}{99}$
The canals of the rete testis (Lauth)	$\frac{1}{166}$ to $\frac{1}{138}$
The tubes in the *anal glands* of the goose	$\frac{1}{93}$
The twig-like cæca or tubes of *Cowper's glands* in the hedge-hog	$\frac{1}{90}$
Cells of the human *Meibomian glands* (Weber)	$\frac{1}{356}$ to $\frac{1}{145}$
Cells in the salivary glands of the murex tritonis, $\frac{1}{6}$ to $\frac{1}{5}$ of a line.	
Cells of the spongy liver of the murex tritonis, $\frac{1}{6}$ to $\frac{1}{4}$ of a line.	

Compare the measurements of different parts, given by Krause in Müller's Archiv. 1837, p. 20.

CHAPTER III.

OF THE PROCESS OF SECRETION.

1. *Of the causes of secretion.*

SECRETION is merely one kind of those changes or "metamorphoses" which the circulating fluid of animals—the blood—undergoes in its course. In all the organs of the body the blood passes through a network of very delicate vessels,—the capillaries—which constitute the medium of communication between the arteries and the veins. The capillaries have no open mouths, but their parietes are extremely thin and delicate,* for the most part imperceptible by the eye, and do not prevent a free interchange of material between the substance of the organ and the currents of blood. The substance of the organ imbibes the blood and appropriates to itself the components of that fluid, assimilating them in a different way in each separate organ.

General conditions of a secreting organ.—All secretions are formed on free surfaces, whether these be afforded by simple membranes, such as the serous and mucous membranes, or by the more complex internal surface of the cellular or tubular cavities of glands. In the secreting membranes the blood is transmitted from the arteries to the veins through an infinite number of anastomosing vessels which form an extended network. The membrane is permeated by the liquid portion of the circulating fluid, effects in it some change, and pours out the matter thus changed as a secretion on its surface.

The most complex gland, with its ducts, canals, tubuli, cells, or cæca, is to be regarded in like manner as merely a very extensive organised surface on which the transformation of the blood takes place.

The elementary tubular canals of the kidney, and the elementary parts of the liver, as well as of the other compound glands, are in their whole course surrounded with a network of capillaries, and are separated from each other merely by delicate cellular tissue, which connects them together, and contains in its substance the minute currents

* See page 217, and the note on the capillaries in the appendix.

of blood. The whole external surface, therefore, of the elementary canals, racemes of cells, tubuli, &c. is overrun with small currents of blood; the walls of the canals, &c. are permeated by its fluid portion, impress on it some peculiar change, and pour out the fluid in its altered state on their inner surface, to be carried out by the efferent duct. This is the simple process of secretion, which differs from nutrition merely in the circumstance that the part of the blood which has undergone the peculiar change is eliminated on a free surface instead of being added to the substance of the organ.

Seat of the secreting process.—It was formerly supposed, in opposition to all analogy, that the secreting process has its seat in the extremities of the glandular canals, or in those mysterious bodies, the acini. But that is a very incorrect view, as Professor E. H. Weber has already remarked; for the acini which in the proper anatomical sense of the word are hollow vesicles, exist in but few of the compound glands; and it would be anything but reasonable to say that the secretion was formed solely at the closed extremities of the branched ducts and tubular canals of other glands, such as the liver and kidneys. Some compound glands, moreover, present in the course of the excretory duct the same elementary parts as at the extremities, whether they be cells, as in the salivary and lachrymal glands of birds and the Meibomian glands of the human subject, or cæca, as in the liver of crustacea and the lachrymal gland of the chelonia. When glands consist of aggregated cæca, the limit between the elementary parts of the gland and the efferent duct cannot indeed be at all indicated. It is therefore extremely probable, indeed certain, that the process of secretion goes on throughout the whole extent of the glandular canals, consequently from one continuous surface.

Mode of exhalation.—The older physiologists were led to imagine the existence of exhalent vessels by their ignorance of that property of animal tissues by virtue of which all matters in solution are imbibed, and transmitted from one part to another, through invisible pores.* But it is now known that the exhalent vessels do not exist, and that, in a secreting surface, the blood-vessels simply form a very close network; the depth at which this network lies, in a membrane not covered with epidermis, has been already shown† to be exceedingly slight. The fluid parts of the blood, circulating in the capillaries, will therefore readily percolate the particles of the special tissue of the secreting membrane, and escape on its free surface, after having undergone a chemical change by its influence. We do not hereby explain the power by which the secretion is thrown off from the secreting surface, but merely the possibility of the fluid finding its way through the coats of the vessels and the membrane. Many secretions are attended with a profuse exudation

* See page 242. † Page 245.

of fluid, which, like many other phenomena, cannot for a moment be attributed to the force of the heart's action, and the impulse thus communicated to the blood: such a mechanical explanation is by no means satisfactory; for, besides the absence of the heart's action to account for secretion in plants, the cases in which secretion is increased by local irritation, the heart remaining unaffected, would still be quite inexplicable. Another difficulty to be solved is the cause of the escape of the secreted fluid solely on the free surface of the membrane:—Why does not the mucus, for example, collect as readily between the coats of the intestine as exude from the inner surface? Why does not the bile permeate the walls of the biliary ducts, and escape on the surface of the liver as readily as it forces its way outwards in the course of the ducts? Why does the semen collect on the inner surface only of the tubuli seminiferi, and not on their exterior—in their interstices? The elimination of the secreted fluid on one side only of the secreting membrane, namely on the interior of the canals, is one of the greatest enigmas in physiology; it may perhaps be explained by either of the following hypotheses:

1. It may be imagined that the capillaries of the gland are provided with exhalent pores so constructed as to allow fluids to pass through in one direction only, namely, towards the cavity of the glandular canals. But here the difficulty occurs, that this hypothesis presupposes the existence of what cannot be demonstrated, and that we must again suppose that there are other pores in the coats of the capillaries for the passage of the fluids destined for the nutrition of the secreting canals.

2. The more probable supposition is, that by virtue of imbibition, or the general inorganic porosity, the fluid portion of the blood becomes diffused through the tissue of the secreting organ; that the external surface of the glandular canals exerts a chemical attraction on the elements of the fluid, infusing into them at the same time a tendency to unite into new combinations, and then repels them, in a manner which is certainly quite inexplicable, towards the inner surface of the secreting membrane or glandular canals.* That the process which we are endeavouring to explain does not consist merely in exudation, but is dependent on an action of the secreting membranes, is evident from the quantity of the fluid poured out by a stimulated salivary gland, and from the suddenness and abundance of the secretion of tears excited sometimes by momentary impressions.

Although quite unsupported by facts, this theory of attraction and repulsion is not without its analogy in physical phenomena; and it would

* Compare the observations of Mascagni on this subject: "Nova per poros inorganicos secretionum theoria vasorumque lymphaticorum historia iterum vulgata et parte alterâ auctâ, in quâ vasorum minimorum vindicatio et secretionum per poros inorganicos refutatio continetur." Auct. P. Lupi. Romæ, 1793.

appear that very similar powers effect the elimination of the fluid in secretion, and cause it to be taken up into the lymphatics in absorption. It is an extraordinary circumstance that, frequently, in different component tissues of the same membrane, both processes are going on within a very small space; that in the mucous membranes, for example, the mucous follicles, which secrete, are closely surrounded by the lymphatics, which attract and absorb.

Dr. Wollaston supposed that secretion was attended with electrical action. He relates the following experiment: a glass tube two inches in length, and $\frac{3}{4}$ of an inch wide, was closed at one end with bladder, and partly filled with water containing $\frac{1}{240}$ of common salt. The bladder was moistened on the exterior and placed on a plate of silver; a zinc wire being now connected by the one end with the plate of silver, and by the other brought in contact with the water, pure soda appeared on the outer surface of the bladder. Eberle,* however, found a stronger galvanic influence necessary to produce this effect.

The cause of the peculiarity, and difference of secretions can be found in no external and mechanical conditions. They have been attributed to difference in the rapidity of the blood's motion in the different organs; but it should first be proved that the rapidity of the blood's motion does differ in this way. They have been ascribed, again, to different states of the blood-vessels, and to the particular angles at which they divide; but it may be seen in Lieberkuehn's preparations that the blood-vessels in the kidneys divide nearly in the same way as in the testes, and in the salivary glands not far otherwise than in the liver; in all parts reticulated capillaries are seen forming anastomoses between the arteries and veins. Others, again, have endeavoured to account for the differences of secretions by differences in the free ends of the arteries, but we have shown that arteries have no free extremities with open mouths. Others attribute a great influence to the different diameters of the canals which receive the secretions, and yet the most various and peculiar fluids are secreted on plane membranes. All these circumstances, on which Haller has laid far too much stress, even if they existed, would not be sufficient to explain the difficulty; and they are not supported by facts. Besides, how easily may all such mechanical explanations be dismissed by the simple question:—What gives rise to the formation of brain on the one hand, of muscle on the other, and, again, in another case of bone? Does the brain also depend for its formation on a peculiar angle of division of the blood-vessels?

The peculiarity of secretions does not depend on the internal conformation of the glands; for, as I have sufficiently demonstrated, each secretion is in different animals the product of the most various glandular structures, and very different fluids are secreted by glands of simi-

* Physiologie der Verdauung, p. 137.

lar organization.* The nature of the secretion depends therefore solely on the peculiar vital properties of the organic substance which forms the secreting canals, and which may remain the same however different the conformation of the secreting cavities may be; while it may vary extremely although the form of the canals or ducts remains the same. The variety of secretions depends, therefore, on the same cause as variety of the formation and life of organs generally; the only difference being that, in nutrition, the part of the blood which has undergone the peculiar change is incorporated with the organ itself, while in secretion it is eliminated from it.

Several chemists, and especially Chevreul, have recently laboured to prove that all secretions are formed independently of any change effected by the organ in the components of the blood; that all the materials of the different secretions pre-exist in the blood itself; and that the principal action of the secreting organ is merely to attract these matters from the blood, and to transfer them to the fluid secreted. As circumstances favouring this view very strongly, Gmelin mentions, that the salts of the blood and those of the secretions are nearly identical; that, both in the blood and in the secretions, osmazome, and a substance resembling salivary matter, occur; and that many of the substances which were formerly believed to exist only in the secretions, namely, casein, cholesterine, stearine, elain, and elaic acid, have been discovered in the blood. The existence of cholesterine in the blood has been recently confirmed anew by Boudet.† Nevertheless the theory appears to me to be founded on a very erroneous view: for, in the first place, neither horn, mucus, biliary matter, picromel, semen, true casein, true salivary matter, nor the poisonous matters secreted by animals, are contained in the blood; and secondly, components of the secretions may accidentally re-enter the blood by imbibition, so that their presence in it is no proof of their being natural constituents of it; and, in fine, the existence of all the secreted matters in the blood would not do away with the difficulty, for it would remain to explain how they were formed in it, we will say, in the blood of herbivorous animals. It is, indeed, quite certain that the "true secretions," as distinguished from the "excretions,"‡ are, like the solid parts of the body, formed from the more simple constituents of the blood by the organs which secrete them.

The *chemical process of secretion* is not at all understood. The simple problem to be solved, is how the secreting membranes can, at the same time, and from the same blood, nourish themselves,—that is, attract analogous particles and add them to their own substance,—and also secrete or eliminate the non-analogous particles; for the secreted fluid is in its chemical properties wholly different from the secreting organ. The

* See the description of the glands in different animals, page 445—456.

† Essai critique et expérimental sur le Sang. Paris, 1833. ‡ See page 429.

glandular substance consists, generally, merely of uncoagulated albumen, which, when reduced to a state of minute division, is readily soluble in water. The elementary parts of a secreting organ are, as far as I have observed, of a grey, greyish-white, or yellowish-white colour; thus, even in the liver of the embryo, the biliary canals seen on the surface of the organ are of a yellow-white colour, and it is only owing to the reticulated capillaries that the liver has a brown aspect; yet the bile is green. In oviparous animals the urine is white, but the substance of the kidneys is totally different: in very young birds just escaped from the shell the minute urinary canals can be seen on the surface of the kidneys, filled with the white urine, as if injected; while the appearance of the rest of the organ is very different. Berzelius did not detect in the substance of the kidney the peculiar chemical constituents of the urine.* The substance of the liver is, it is true, found to contain fatty matters which are components likewise of the bile, and in disease it is prone to become converted into fat; but the essential constituents of the bile have not been detected in it. Braconnot's analysis of the liver† shows that its composition is very different from that of the bile; and Kuehn‡ has obtained from the liver a fatty matter which differs by very marked characters from cholesterine. Besides, it must be remembered that it is almost impossible to obtain any of the substance of the organ entirely free from bile. But, restricting ourselves to the "secreting membranes," we find that the skin, for example, contains no horny matter, and yet it secretes that substance; and the tissue of the choroid, when washed, seems itself to contain no pigmentum nigrum.

It is therefore certain that the matter secreted differs in its chemical properties from the organ which forms it, and that secretion cannot be a mere liquefaction of the substance of the organ; that, on the contrary, the substance of the secreting surface, while it attracts to itself analogous matters from the blood for the purpose of nutrition, at the same time separates from it something that is non-analogous.

In the nutrition of organs which afford no secretion, those components of the blood which are analogous to the tissue are attracted by it, while the non-analogous components re-enter the circulation; in the process of secretion non-analogous matters are thrown off and carried out of the body.

It might then be imagined, that each molecule of blood which comes under the decomposing influence of a secreting organ, is completely decomposed and disposed of by it; so that those of its elements which go to the nutrition of the organ, and those which form the secretion, would, reunited, produce blood. If the molecule of blood is expressed by the sign a, and a molecule of the component matter of the secreting organ by x, the secretion would, according to the above supposition, be

* Berzelius, Chimie Animale, translated by Jourdain, p. 333.

† See page 371.

‡ Kastner's Archiv. xiii. p. 337.

a—x. We have no data to determine whether this hypothesis is correct or not; therefore I will not adopt it, but mention it merely as an idea worthy of consideration in further researches. It is a simple and therefore attractive hypothesis, but is at once seen not to be applicable in the case of those secretions in which the matters separated from the blood have—as urea, for example,—been formed in other parts of the body.

That the secretion undergoes a further change—that its formation is perfected—in its passage through the narrow and often very long canals of the glands, may be conceived to be possible, but is not susceptible of proof. There has always been a disposition to admit this supposition in the case of the testis; but since the tubuli of the kidney are as long as those of the testis, while the urine is a mere excretion and does not require any further elaboration, it is evident that the length of the tubes has a more important relation to the extent of the secreting surface than to the production of any further change in the fluid already secreted.

The *chemical composition of the individual secretions* offers at present little of interest in relation to the general physiology of secretion, and is important only in connection with the several functions in which they are implicated; the "secreta" therefore are treated of in the sections devoted to those functions. The secretions, "secreta," which are met with more generally throughout the body,—fat, mucus, and synovia,—are described with the secreting membranes; the bile, saliva, the gastric and pancreatic secretions, in the section on digestion; the urine and perspiration under the head of the excretion; semen, milk, &c. with the subject of generation.

The *microscopic globules found in some secretions*, as the semen and milk, for instance, are important. I have observed in the bile of the frog very scanty granules unequal in form and size, the largest about five times smaller than the red particles of the animal's blood; the green colouring matter of the bile, however, is in solution; Weber also describes granules as existing in the bile. I have likewise found granules in very small number in the saliva; Weber finds them to be larger than the red particles of the blood, and transparent: the greater part of the solid matter of the saliva is in solution. Weber could discover no globules in the perfectly transparent portion of mucus; he saw only the ordinary flakes of the mucus. It appears to me that by far the largest proportion of the components of the saliva, bile, and mucus, as well as of the urine, are in solution; while in the semen, milk, pigmentum nigrum, and pus, on the contrary, there are granules in such number that they must be looked upon as among the most essential ingredients of these fluids. The granules of the pigmentum nigrum are, according to Weber, of unequal size, but in the mean about $\frac{1}{7388}$

of an English inch; they are therefore about half as large as the red particles of the blood. The globules of the milk are described by Weber to be very transparent, and round, but irregular in size; in the mean $\frac{1}{3}$ or $\frac{1}{2}$ smaller than the blood particles. Treviranus remarks, that they do not sink in the fluid and that they refract the light strongly, and hence infers that they are globules of fat. Weber regards them as composed of caesin and fatty matter. The pus globules are, according to Weber, round, and measure from $\frac{1}{2770}$ to $\frac{1}{1385}$ of an inch in diameter, the size of the majority being $\frac{1}{2215}$ of an inch; they are therefore about twice as large as the red particles of the blood. All the foregoing facts prove that the globules of the secreted fluids are not red particles of the blood which have undergone a change; the globules of the milk are too small, those of the pus too large; the latter cannot come from the interior of the capillary vessels, for their diameter is greater than that of the smallest of these vessels. Besides, if red particles which were thus altered could find their way out of the vessels, others in the unchanged state would escape with them. The view which I take of the mode of production of the globules of the milk, pigmentum nigrum, and pus, is, that they are either thrown off from the substance of the secreting surface, or formed by the partial coagulation of the animal matter dissolved in the secretion into globules, (in a way similar to the coagulation of albumen in solution,) which is probably the mode in which the particles of the milk and pigmentum nigrum are produced. With respect to the origin of the globules of the pus, Autenrieth* relates the following remarkable observation. If some of the watery moisture which exudes from the surface of an inflamed part after the pus has been removed, is collected between two transparent thin plates of talc and allowed to lie in the wound, globules are seen to form gradually in it, to enlarge and become opaque; while, if the fluid is removed altogether from the atmosphere of the living textures, no such change takes place in it. Brugmans† also states, that if a suppurating surface has been washed clean, the pus is seen to be secreted as a clear fluid, which afterwards becomes thick and opaque.‡

2. *Of the influence of the nerves on secretion.*

There is at present little known concerning the influence of the nerves on the process of secretion. The experiment instituted by the Baron A. Von Humboldt on his own person, is well known. Having applied two blisters to the region of the shoulders, he covered one of the blistered surfaces with a silver plate, and closed the circle by means of a con-

* Physiol. ii. 119.

† Diss. de Pyogenia, 114.—Schroeder Vander Kolk, Observ. Anat. Pathol. 21.

‡ On the subject of this section, consult Wedemeyer, über den Kreislauf des Blutes; Doellingir, Was ist Absonderung? Würzburg, 1819.

ductor of zinc, when a painful burning was produced, and a change in the character of the discharge; from being bland and colourless, it became a red acrid fluid, which left livid, red streaks on the parts of the back where it ran.* M. Most† likewise states, that, having caused a galvanic current to pass through the parotid, by applying the positive pole to the situation of the gland for the space of ten minutes while he held the negative pole in his hand, an increased secretion of saliva, which was neither acid nor alkaline, took place.

The influence of the nerves on secretion has as yet been made the subject of but few direct experiments; but it is certain that, after division of the nervus vagus, the secretion of gastric juice ceases.‡ Brodie§ has shown, by a series of experiments, that, when the nervus vagus and nervus sympatheticus have been divided, arsenic does not give rise to the copious secretion in the stomach and intestines which usually follows its exhibition. The secretion of the pulmonary mucous membrane also is altered by division of the vagus; hence the frothy bloody exudation which is found in the lungs after that operation.

Krimer has instituted some experiments relative to the influence of the nervous system over the secretion of urine, an influence which is proved to exist by the circumstance that nervous affections are usually attended with secretion of limpid urine containing an unnaturally small proportion of its proper ingredients. Krimer || states, that on examining the state of the urinary secretion after having divided the nerves of the kidneys, he has found it contain albumen and the red colouring matter of the blood, their proportion increasing in the same degree as that of the proper constituents of the urine decreased. Division of the vagus did not put a stop to the secretion of urine; but rhubarb and prussiate of potash taken by the mouth ceased to pass off by the urine, which at the same time acquired greater specific gravity from containing serum of the blood: when the divided nerves, however, were connected with the galvanic pile, the urine reacquired its normal character, and the substances above mentioned showed themselves again in it. After division of the spinal cord in the dorsal or lumbar region, the urine became limpid like water. While division of the sympathetic nerve in the neck caused it to become alkaline and albuminous; and on the application of galvanism, its normal properties were restored. Brachet ¶ has made similar observations on the effects of interrupting the trans-

* Ueber die gereizte Muskel und Nerven-faser, i. 324.

† Ueber die grossen Heilkräfte des Galvanismus. 1823.

‡ Tiedemann und Gmelin, die Verdauung, i. 340. The French translation by Jourdain, pt. i. p. 372.

§ Phil. Trans. 1814, p. 104.

|| Physiol. Untersuchungen. His experiments are given in Lund's Physiolog. Resultat. der Vivisect. neuerer Zeit. Kopenhagen, 1825, p. 204.

¶ Récherches Experiment. sur les fonctions du Syst. Nerv. Ganglion. Paris, 1830, p. 269.

mission of nervous influence to the kidney. He divided the renal artery of a dog, and then connected its two portions by means of a cannula, so that the renal nerves were divided, but the supply of blood maintained. The fluid, which flowed from the ureter during several hours succeeding the operation, was red, and separated into a fibrous coagulum and serum. Repetition of the experiment was attended with the same result. Division of the nervi vagi had no effect on the secretion of urine.

I have recently, in conjunction with Dr. Peipers, instituted a series of experiments on dogs and sheep, to determine the influence of the nerves in secretion. We applied a ligature to the renal vessels (the ureter being excluded), and tied it so tightly that the texture of the renal nerves included in it should at that point be destroyed. We then loosened the ligature again, so that the circulation of the blood through the kidney was re-established. The ureter was brought to the exterior of the body and a tube connected with it. In most cases the secretion of urine was completely arrested, even when the same operation was performed on the second kidney (in a sheep), and the ligature retained on that side to render the secretion of urine there quite impossible. Once only, namely, in a sheep, the secretion continued in the injured kidney; but the fluid was bloody, and M. Wittstock found that it contained hippuric acid. The softening of the substance of the kidney which always ensued on the performance of these experiments, which were often repeated, was very remarkable.*

The influence of the nerves on the glands may be of a different nature in each gland, or, which is more probable, it may be the same in all, merely enabling the secreting substance, in each gland endowed with peculiar properties, to exert its chemical action. Daily experience affords us many proofs of the influence of the nerves on secretion. We know that, during the depression of the nervous system in the cold stage of fever, not only the quantity of all the secretions, but also the proportion of the natural ingredients in them, are diminished; and that, with the accession of the hot stage, the secretions are restored. We also know that dryness of the mucous membranes and of the skin are often signs of depressed nervous influence in acute diseases. How frequently, too, do we observe the influence of passions of the mind on secretion, for example, on the secretion of the tears, of the bile, and the milk, and even on the secretion and other conditions of wounds.† It has indeed been stated that the presence of the foal has an effect on the secretion of milk in the mare. I will not lay stress on the accounts of the poisonous action of the saliva of enraged animals; for the phenomena observed in such cases to follow the bite are generally, perhaps, merely those

* Peipers, de Nervorum in Secretion. Actione, Berol. 1834.

† See page 374.

dependent on the form of the wound: but it is a well-known and undoubted fact, that not merely the presence of food in the mouth causes an increased flow of saliva, but that even the sight of savoury food excites the salivary secretion. If it were possible wholly to cut off the nervous influence of a secreting organ, we should find perhaps, as after division of the nervus vagus in reference to the gastric juice, that the function of the special secretions is wholly arrested by the interruption of nervous energy. I am far from believing that the power of chemical action, which the glandular substance owes to its state of life, has not an equally important share as the nervous influence on secretion; but it is probable that the influence of the nerves is necessary for the support of this chemical action, which in each gland is different.

On a first view, the cerebro-spinal, as well as the sympathetic nerves, appear to have the function of regulating secretion. The distribution of the lingual nerve in the submaxillary and sublingual glands, of the glosso-pharyngeal nerve in the tonsils, and of a branch of a tibial nerve in the capsule of the knee-joints, are well-known anatomical facts. It is a most remarkable fact, that the female mammary gland receives its nerves, not directly from the sympathetic, but, as it appears to me, only from the third and fourth intercostal nerves. It is extremely probable, however, that the cerebro-spinal nerves are accompanied by fibres of the sympathetic; indeed Retzius has shown this to be the case with the second branch of the fifth nerve in brutes, and in them it is evident also in the case of the nervus buccinatorius, which has many grey nerves, derived from the otic ganglion, running over it. In hemiplegia from disease of the brain or spinal marrow, the secretion of the surface on the affected side is sometimes altered, sometimes not.

3. *Of the changes of which secretions are susceptible.*

The process of secretion may be disturbed from local, as well as from general causes.

The state of the secreting organ affects not merely the quantity, but even the quality of the secretion: the urine is watery, and contains less of its proximate components, after nervous attacks; the mucus secreted in the different stages of a catarrh is very different,—at first it is watery and salt, afterwards thicker; the inflammation at length generally arrests entirely the special secretion of every secreting organ, as it does the function of other organs. Stimulants or irritation affect secreting organs in a peculiar manner; at first the secretion is increased in quantity, but, in proportion as the irritation passes into inflammation, the state of increased action diminishes. When secreting organs become relaxed, and their texture loose, the secretion is generally increased in quantity, but diminished in consistence, it becomes more watery; when

they are relaxed, and at the same time their texture thickened, the secretion is lessened in quantity. This observation applies to all secreting organs, the mucous membranes of the nostrils, the conjunctiva, and the skin. Morbid secretions are subject to the same law: an ulcer when stimulated affords a copious secretion of pus; if it becomes highly inflamed, the secretion is stopped; if the ulcer is relaxed,—its walls loose and flabby,—it secretes a copious watery fluid; while if, at the same time that its action is feeble, its tissue is thickened by the deposition of the products of inflammation, the secretion formed by it is very scanty.

Interruption of nervous influence causes diminution of the quantity of the natural secretion of a secreting organ; in nervous attacks the urine is limpid, watery; in fevers, with depressed state of the nervous energy, and in the cold stage of all fevers, the skin is dry. But it is extraordinary, that a much more complete arrest of the nervous energy,—such as occurs in syncope, and under the influence of terror,—can give rise to an unusually copious secretion on the skin, producing cold sweat, and, in the latter case, in the intestines, giving rise to diarrhœa. We are acquainted with the changes produced in the composition of secretions, in consequence of affections of the nervous system, rather by their injurious effects,—for instance, by the effects of milk and bile secreted after the mind has been the subject of violent emotions,—than by any chemical examination to which they have been submitted.

Since all secretions, inasmuch as they extract certain ingredients from the blood, produce a change in its composition, no one secretion can be altered in quantity or quality without disturbing the balance which exists between all in their action on the blood; hence, the increase of one secretion gives rise to the diminution of another. On the principle of this relation between the different secretions, or their "antagonism," as it is called, depend, in many instances, the practice of exciting artificial discharges to put a stop to morbid secretions. The antagonism of the secretions is observed to be subject to the following laws:

1. The increase of a secretion in a tissue, A, which is less irritable than the organ, B, is incapable of producing a diminution in the secretion of the latter; hence, for example, artificially excited secretions from the skin, as by a blister, in the neighbourhood of the eye, in inflammations of the latter organ, are of no service, because the eye is a more irritable part than the skin.

2. An increased secretion in a certain tissue, A, cannot be diminished by exciting the same secretion in another part of the same tissue, A; on the contrary, such a procedure would rather increase the secretion from all parts of the tissue than diminish it, because the relation which exists between the different parts of one and the same tissue is that of sympathy, not of antagonism. Hence, a discharge from the generative or

urinary organs cannot be arrested by an artificially excited diarrhœa.

3. On the contrary, the secretions of tissues which do not belong to the same class of structures, often antagonise each other. Thus, increase of the cutaneous secretion frequently induces diminution of the secretion of the kidneys: in summer the cutaneous exhalation is more abundant, and the urinary secretion proportionally scanty; in winter the reverse is the case. Effusion of watery fluids into the cellular membrane and serous cavities is attended with dryness of the skin and diminution of the urinary secretion, the quantity of which is observed to increase in the same proportion as dropsical effusions diminish. Suppression of the exhalation from the skin by cold, gives rise to mucous discharges from the intestinal and pulmonary mucous membranes.

4. It is only towards the termination of consumptive diseases that this relation of antagonism between the secretions ceases to exist, when, in consequence of the relaxed state of the tissues, all are at length increased in quantity; in the colliquative state that precedes death in phthisical patients, colliquative diarrhœa, profuse sweating, and dropsical effusions take place simultaneously.

5. When one tissue is excited to increased action by an impression made upon another, either the secretion of the two must have been in some respects similar, as in the case of the skin and kidneys, both of which have the office of excreting water from the blood; or the organ thus excited must have had a predisposition to morbid action, which is the rational explanation for the circumstance, that the impression of cold produces in one person an affection of the mucous membrane of the lungs, in another, a disordered secretion of mucus in the intestinal canal.*

Sometimes the suppression of a secretion in one part of the body gives rise to the appearance of the same fluid in another part. This happens most frequently with those matters which exist in the blood previously to the act of excretion. Effusions of blood, vicarious of the menstrual flux, have certainly occurred; and the total destruction of both kidneys, by preventing the elimination of the urea already present in the blood† by the ordinary channel, must be calculated to induce effusions of fluids impregnated with urea in all the other parts of the body. Nysten‡ has ascertained the existence of urea in fluids formed in other parts during the total suppression of the renal secretion; and

* Consult Heusinger, über den Antagonismus der Excretionen, in his Zeitschrift für organ. Physik. Bd. i.

† See page 151.

‡ Récherches de Chim. et de Physiol. Pathol. Paris, 1811, page 263—293.

it is an undoubted fact that urate of soda is contained in the depositions of gout.

If, however, the essential ingredient of the secretion does not exist in the blood itself, the suppression of this secretion in the organ destined to form it cannot cause its metastatic appearance in other parts; the instances which have been adduced of such an occurrence are ill-supported by proofs.*

The sole secretion, of which the constituents do not exist as such in the blood, but which can nevertheless be formed at all times and in all parts of the body, is pus, the organ for its production being generated anew in the process of inflammation.

In the cases in which the total suppression of a secretion gives rise, by an antagonistic influence, to the production of another, of which the ingredients cannot be derived ready formed from the blood, the new secretion is always essentially different from the one of which it balances, as it were, the suppression, and resembles it only so far as is compatible with its natural proximate elements. True vicarious secretion of milk, for example, never occurs. Autenrieth has remarked that such supposed secretions of milk from other organs do not contain the essential components of milk, namely, the sugar of milk and butter. They contain only those proximate components of the blood which might have served for the formation of milk, such as albumen, for example. We have already shown the fallacy of the views relative to the supposed metastatic secretion of pus.†

The glandular secreting canals pour out the product of their chemical action on their interior surface only.‡ It is only in very rare cases—as in the form of jaundice excited by affections of the mind,—that the newly-formed matter seems to be again carried into the circulation.

4. *Of the discharge of the secretions.*

The *efferent ducts* of glands are lined by a mucous membrane, which has on its exterior an extremely thin layer of muscular substance. The existence of muscular fibres cannot, it is true, be demonstrated anatomically, but physiological observations place it beyond dispute; the efferent ducts of most glands have the power of contracting when irritated. The contractile power of the ductus choledochus in birds was known to Rudolphi. By irritating mechanically or by galvanism the ductus choledochus of a bird just dead, I have frequently produced a very strong contraction of it, which continued some minutes, after which the duct resumed its previous state. I have often excited strong local contractions of the ureters likewise, both in birds and rabbits, by the application

* See page 431. † See page 277.

‡ See the remarks on this law at page 461.

of a powerful galvanic stimulus. Tiedemann* also has seen motions of the vas deferens of a horse ensue on the application of a stimulus. It appears, indeed, that periodic vermicular motions are performed by the efferent ducts, at least by the ductus choledochus in birds; for I have once observed in a bird just killed contractions of the duct occurring regularly in pauses of several minutes; the tube dilating again in the intervals; and, what was remarkable, the contractions took place in an ascending direction, namely, from the intestine towards the liver: and this seems to throw some light on the mode in which the bile at certain times, instead of being expelled into the intestines, is retained and driven into the diverticulum of the duct, namely, the gall-bladder; the complete closure of the mouth of the duct contributes perhaps to this effect.

The discharge of the bile from the gall-bladder during digestion results probably from the mere pressure of the surrounding parts, and the action of the abdominal muscles, while the mouth of the duct is open: for I doubt if the gall-bladder is contractile; I could produce no contraction of it in mammalia and birds, even with the most powerful stimulus of a galvanic battery; and in this respect it differs from the other diverticula of efferent ducts, namely, the urinary bladder, and the vesicula seminalis, which it resembles in all other characters.

The nature of the internal coat of the efferent ducts, and the contractility of their middle coat, prove most clearly that they are merely diverticula of the membranous tubes into which they lead; thus, the ductus choledochus and pancreaticus, consisting as they do of the same membranes as the duodenum, are prolongations of its coats.

How far the contractility of the ducts may contribute to the frequently sudden expulsion of the saliva and tears, is a question which I mention merely as requiring further investigation. I may, in conclusion, remark, that since the contractility of the ducts of glands is proved experimentally, the spasm of these parts, spoken of by physicians, ceases to be a mere hypothesis.

* Ueber die Wege, auf welchen Substanzen aus dem Magen und Darm-kanal ins Blut gelangen, p. 22.—Récherches sur l'Absorption; traduit par Heller. Paris, 1821.

SECTION IV.

*Of digestion, chylification, and the excretion of the decomposed effete matters.**

CHAPTER I.

OF DIGESTION IN GENERAL.

The food of animals consists of animal and vegetable substances. Some animals live solely on the former class of substances, others on the latter; others, again, have a mixed diet, consisting of both animal and vegetable matters. Man is one of the last; he is supported as well by food constituted wholly of animal substances as by that which is formed entirely of vegetable matters; the structure of his teeth, as well as experience, seem to point out that he is destined for a mixed kind of aliment.

Both the vegetable and animal articles of diet contain the more common salts, which, being essential components of the animal system, may in a certain point of view be regarded as nutriment. But no animal can subsist on mineral substances alone; it is only from necessity, or from prejudice, that, to fill the stomach, earth, either alone or mixed with organic matters, is sometimes swallowed by human beings,—for instance, by the Ottomaks and Guamos in Oronoco, and by the inhabitants of Nova Scotia. Vauquelin could detect no nutritious matter in the steatite which is eaten by the inhabitants of Nova Scotia.† The earth which, on account of famine, was, in the year 1832, in the parish of Degernä, on the borders of Lapland, mixed with flour and the bark of trees, and baked so as to form a kind of bread, consisted of silicious earth mixed with organic particles.‡ This mineral flour was found by Retzius to consist of the fossil remains of nineteen different forms of infusoria.

All substances from the animal and vegetable kingdoms appear to afford nutriment, provided that they are easily soluble in the animal fluids, contain no combination of elements too unlike that of the animal matters of the being which it ought to nourish, have no remarkable chemical properties, and no tendency to enter into binary combinations at the expense of the organic components of the living body. All substances which have such a tendency, which are of heterogeneous composition, or have peculiar chemical properties, are either medicinal substances, or, in a relative sense, poisons. I am much inclined to

* These processes are more complicated than those which we have hitherto considered. In treating of them it is necessary to presuppose an acquaintance with the laws of the circulation, absorption, the action of the lacteals and lymphatics, and secretion; the latter processes, which are not confined to the digestive organs, but are carried on in many other parts of the body, have therefore been discussed first, so that we shall not need to enter here into any long explanation of them.

† See Humboldt's Reise in den Equinoct. Gegend. iv. p. 557. Travels in the Equinoctial Regions of the New Continent, translated.—Rudolphi's Physiol. ii. 18.

‡ Poggendorf's Ann. B. xxix. p. 261.

believe that even the peculiar effects of the narcotic poisons which produce no evident material change in the system, and do not essentially excite inflammation, arise from the heterogeneous and peculiar chemical substances which they contain causing decomposition and the formation of binary compounds in the animal matter of the body. This opinion appears to me to be rendered probable by the circumstances that the substances to which we allude contain vegetable alkaloids, and that, according to the observation of Fontana, the most active narcotic poisons —the poison of the viper, and the ticunas,—exert a chemical action on animal substances, an effect which has been observed particularly in the blood.* The term "poison" is to be taken quite in a relative sense. The poison of serpents when introduced into the blood produces decomposition of the animal fluids; but, when taken into the stomach, it is rendered innocuous, being decomposed, as it would seem, in the alimentary canal. The poison of the viper exerts its poisonous influence very slowly likewise, when applied to wounds in the lower vertebrata, particularly in the amphibia—as frogs,—and in the blind-worm; to serpents, it would appear to be innocuous. Most narcotic poisons, however, are, in large doses, destructive even to the lower animals. Prussic acid is as destructive to leeches as to the human subject; opium and nux vomica appear to be poisonous to all animals, with the exception of the bird, buceros rhinoceros, which is said to feed on the nuts of the strychnos.

The most simple nutritive substances from the vegetable kingdom are,

1. The acid juices of many plants and fruits.

2. Starch (amylum),—in the seeds of the grasses and leguminous plants, in the tubera of the potato, in sago, and in lichen Islandicus.

3. Vegetable mucilage—in roots and seeds, and in the form of the different gums. It differs from animal mucus in being soluble in water.

4. Sugar—in the juices of many plants, and of their fruits.

5. Fatty, or fixed vegetable oils—in seeds, and some tuberous roots.

6. Vegetable albumen—in the milky juices of vegetables, in the milk of the milk-tree, brosimum galactodendron,† in seeds which yield emulsions by trituration.

7. Gluten—generally combined with albumen in the different kinds of grain and other seeds, also in sweet fruits.

8. Fungin—in the fungi.

Many other substances,—the spirituous and aromatic substances, for example,—merely stimulate the digestive organs, and do not afford nourishment. The woody fibre, the investments of seeds, most resins, colouring and extractive matters, hairs, feathers, horn, claws, scales, the external skeleton of insects, and all horny substances generally, are indigestible.

* See page 97. For an account of the vegetable poisons, consult works on Toxicology; on animal poisons, see Rudolphi, loc. cit.

† Dr. Don in Ed. N. Phil. Journ. 1829, Oct. Dec.

The principal nutritive principles derived from the animal kingdom are,

1. Gelatin—in the tendons, bones, cartilages, the skin, the cellular tissue, and especially in very young animals.*

2. Albumen—principally in the ova, brain, and nerves, in the blood, &c.†

3. Fibrin—in muscular substance, and the blood.‡

4. Animal oil and fat.§

5. Casein—in milk, with animal fat (butter), and in cheese. Its properties will be described in the 8th Book.‖

Nutritive principle of food.—The end and object of digestion is, *first*, the solution of the food, since nothing can be taken up by the absorbent vessels which is not in solution; and, *secondly*, the reduction of the different ingredients of the food above enumerated into the most simple material of the animal processes, namely albumen, which is found to be contained in the fluid resulting from the digestion of the food, partly in the state of solution, and partly in globules. The essential character of the digestive process, then, consists in its not only effecting the solution of the food, but in its likewise annulling the peculiar properties which the nutritive matters may owe to the source whence they are derived; that is to say, in its dissolving the food, and converting all into albumen. To effect these changes, something more than mechanical division, chemical influences,—digestive fluids,—are necessary. Those substances, then, are most easy of digestion, and most nutritious, which are most easily soluble and most readily converted into albumen, or which themselves contain albumen; and hence we see that the yolk of the egg, being a concentrated solution of albumen (with oil) forms for the embryo a nutriment which is assimilated immediately without any previous digestion. Every thing, on the other hand, is indigestible, which —like woody fibre, and the skin of fruits, for example,—can, on account of its insoluble nature, afford no nutriment, or itself exerts a chemical action which calls into play the tendency of the elements of the organic matter to form binary compounds, a tendency which had been previously counterbalanced by the organic force. A distinction must be made also between substances easy of digestion and nutritious substances. A substance may, by reason of its solubility, be in that sense easy of digestion, and yet afford little nourishment, its composition being such that it is with difficulty converted into albumen. Other substances, which, when once dissolved, are very nutritious, may, on the other hand, be difficult of solution, and thus indigestible for weak digestive powers. Good food, therefore, must not only be easy of solution, but also nutri-

* See page 133, and Appendix.

† See page 129.

‡ See page 125.

§ See page 131 and 433.

‖ A full account of all the substances used as food is contained in the third volume of Tiedemann's Physiologie. Darmstadt, 1836.

tious in its nature. The further a substance is removed in its composition from that of albumen the less nutritious will it be, and the greater expenditure of the digestive powers is required for its conversion into chyle.

If digestion consisted merely in the solution of the food, and if all articles of diet contained a certain quantity of one and the same nutriment, for which no further chemical change was required, the quality of any article of food might be determined by ascertaining its degree of solubility, the quantity of nutriment which it contained, and the degree of difficulty attending the extraction of this nutriment from the other ingredients of the substance. The dogma of Hippocrates that there are different kinds of food, and but one kind of nutriment (alimentum), is founded on this incorrect conception of the nature of nutriment. Some of the substances which are taken as food, and which must be converted into albumen,—the vegetable substances, for instance,—themselves contain, before they are digested, no albumen. "Alimentum," in the sense in which the term is used by Hippocrates, is therefore the product of digestion; to afford which, those substances that differ in their composition from albumen require to undergo in the stomach a chemical change.

Azotized and unazotized aliments.—M. Magendie has pointed out* an important distinction which may be made in the alimentary substances, between those which contain nitrogen and those in which it constitutes little or no part.

The substances which contain little or no nitrogen are the saccharine and acid fruits, oils, fats, butter, mucilaginous vegetables, refined sugar, starch, gum, vegetable mucus, and vegetable gelatin. The different kinds of corn, rice, and potatoes, are aliments of the same kind. The azotized aliments, on the contrary, are vegetable albumen, gluten, fungin, and some matters met with in different plants, which resemble osmazome: these azotized vegetable principles are met with principally in the seeds of the grasses, and in the stems and leaves of the grasses and herbs, the seeds of leguminous plants — lentils, peas, and beans; almonds and nuts also contain them. Of the animal substances which contain nitrogen the chief are gelatin, albumen, fibrin, and casein. Most animal substances, with the exception of fat, contain more or less nitrogen. Some writers have supposed that respiration is the source whence the nitrogen of the animal body is derived, while others have imagined that it is generated from other elements. The instance of the herbivorous animals which feed on substances that contain little or no nitrogen, and that of the negroes, who live for a long time on a diet consisting entirely of sugar, have been adduced in support of the latter opinion. M. Magendie, however, observes that almost all the vegetables which afford

* Physiol. edit. 2. t. ii. p. 486. Milligan's Translation, 4th edit. p. 223.

nourishment to animals and man contain more or less nitrogen, that this element enters in pretty large quantity into the composition of impure sugar, and lastly, that the nations which feed on rice, maize, or potatoes, take also milk or cheese.

Very valuable experiments have been instituted by M. Magendie to determine the degree of nutritive property possessed by substances which contain no nitrogen,—by a food, for example, consisting wholly of sugar and distilled water. The experiments were performed on dogs. During the first seven or eight days the animals were brisk and active, and took their food and drink as usual: in the course of the second week they began to get thin, although their appetite continued good, and they took daily between six and eight ounces of sugar. The emaciation increased during the third week, and they became feeble, and lost their activity and appetite. At the same time an ulcer appeared on each cornea, followed by an escape of the humours; this took place in repeated experiments. The animals still continued to eat three or four ounces of sugar daily, but nevertheless became at length so feeble as to be incapable of motion, and died on a day varying from the 31st to the 34th. (And it must be recollected that dogs will live the same length of time without any food at all.) After death the muscles were found very much wasted, the stomach and intestines much contracted, the gall-bladder and urinary bladder distended. The urine was analysed by Chevreul, and found to be alkaline, as in herbivorous animals, and to contain no uric acid or phosphates. The bile contained abundance of picromel, which also exists in large proportion in the bile of herbivora, but which has been recently found to be likewise present in the bile of carnivorous animals. The fœces contained but little nitrogen, which generally forms a large part in their composition. To ascertain whether these effects are peculiar to a sugar diet, or result from the want of nitrogen, Magendie kept dogs on olive-oil and water. All the phenomena produced were the same, except that no ulceration of the cornea took place. The same was the result when dogs were fed on gum alone, which is a very nutritious substance if taken mixed with other aliments, but which contains no nitrogen. With butter the effects were the same, and the dog died on the thirty-sixth day, although meat was given him on the thirty-second day; one eye ulcerated; and the urine and bile were found in him, as well as in the dogs fed with gum and oil, to be of the same composition as in those fed on sugar. By other experiments Magendie ascertained that both from sugar, oil, and gum, chyme and chyle are formed, and that consequently it is not from want of being digested that these substances do not nourish the animals. In addition to the experiments here detailed, the fact may be adduced that in Denmark a diet of bread and water for four weeks is considered equivalent to the punishment of death; and that Dr. Stark died, in consequence

of experiments which he instituted on himself, to determine the effects of long-continued sugar diet: after taking such food for some months, he became extremely feeble and swollen, and red spots appeared on his face, and threatened to break out into ulcers.

Magendie's experiments have thrown some light on the causes and mode of treatment of gout, and calculous disorders. The subjects of these diseases are generally persons who live well, and eat largely of animal food: most urinary calculi, gravelly deposits, the gouty concretions, and the perspiration of gouty persons, contain abundance of uric acid, a substance into the composition of which nitrogen enters in large proportion. By diminishing the proportion of azotized substances in the food, the gout and gravelly deposits in the urine may be prevented.

Tiedemann and Gmelin have confirmed Magendie's experiments. They fed different geese, one with sugar and water, another with gum and water, and a third with starch and water. All gradually lost weight. The one fed with gum died on the sixteenth day; that fed with sugar on the twenty-second; the third, which was fed with starch, on the twenty-fourth, and another on the twenty-seventh day; having lost during these periods from one-sixth to one-half of their weight. But a goose which was fed with boiled white of egg cut into small pieces, although it maintained its appetite, and the food contained nitrogen, also died on the forty-sixth day, after having lost nearly one-half its weight. These experiments of Tiedemann and Gmelin, like those of Magendie above detailed, would be very conclusive if the same animals had been fed alternately on different substances that contained no nitrogen; for the experiments of Magendie, which follow, show that animals are frequently not able to support a diet consisting constantly, without change, of one and the same substance, though it contain azote.*

Necessity of the variation of diet.—Magendie's further experiments on the nutritious property of different substances, establish the following facts:—1. A dog fed on white bread, wheat and water, did not live more than fifty days. 2. Another dog, on the contrary, which was kept on brown soldier's bread, did not suffer. 3. Rabbits and Guinea-pigs fed on any one of the following substances,—wheat, oats, barley, cabbage, or carrots,—died with all the signs of inanition in fifteen days; while, if the same substances were given simultaneously, or in succession, the animals lived without suffering any ill effect. 4. An ass fed on dry rice, and afterwards on boiled rice, lived only fifteen days. A cock, on the contrary, was fed with boiled rice for several months with no ill consequence. 5. Dogs fed with cheese alone, or with hard eggs, lived for a long time; but they became feeble and thin, and lost their hair. 6. Rodent animals will live a very long time on muscular substance. 7. After an animal has been fed for a long period on one kind of aliment, which, if

* See Londe, Froriep's Notiz. Bd. xiii. No. 10.

continued, will not alone support life, allowing him his customary food will not then save him: he will eat eagerly, but he will die as soon as if he had continued to be restricted to the one article of food which was first given. The conclusion to be deduced from the above facts is, that difference and variety of the kinds of aliment is an important circumstance to be attended to in the preservation of health.

Dr. Prout reduces all the articles of nourishment among the higher animals to three classes: 1. the *saccharine,* comprehending sugar, starch, gum, &c.; 2. the *oily,*—including oils and fats; and 3. the *albuminous,*—the proximate principles of animals and vegetable gluten. The following account of his views, an extract from a treatise not yet published, is given in Dr. Elliotson's translation of Blumenbach's Physiologie, and quoted from the latter work in Mayo's Outlines of Human Physiology.

"Observing that milk, the only article actually furnished and intended by nature as food, was essentially composed of three ingredients, viz. saccharine, oily, and curdy or albuminous matter, I was by degrees led to the conclusion that all the alimentary matters employed by man and the more perfect animals might, in fact, be reduced to the same three general heads; hence I determined to submit them to a rigorous examination in the first place, and ascertain, if possible, their general relations and analogies.

"An account of the first of these classes, viz. the saccharine matters, has been published in the *Philosophical Transactions,* and the others are in progress. The characteristic property of saccharine bodies is, that they are composed simply of carbon united to oxygen and hydrogen in the proportion in which they form water; the proportions of carbon varying in different instances from about thirty to fifty per cent. The other two families consist of compound bases (of which carbon constitutes the chief elements) likewise mixed with and modified by water, and the proportion of carbon in oily bodies, which stand at the extreme of the scale in this respect, varies from about sixty to eighty per cent.; hence, considering carbon as indicating the degree of nutrition, which in some respects may be fairly done, the oils may be regarded in general as the most nutritious class of bodies; and the general conclusion from the whole is, that substances naturally containing less than thirty, or more than eighty per cent. of carbon, are not well, if at all, adapted for aliment.

"It remains to be proved whether animals can live on one of these families exclusively; but at present experiments are decidedly against this assumption, and the most probable view is that a mixture of two at least, if not of all three, of the classes of nutriment is necessary. Thus, as has been stated, milk is a compound of this description, and almost all the gramineous and herbaceous matters employed as food by animals contain at least two of the three—the saccharine and glutinous, or albuminous. The same is true of animal aliments, which consist at least of the albu-

minous and oleaginous: n short, it is perhaps impossible to name a substance employed by the more perfect animals as food, which does not essentially constitute a natural compound of at least two, if not of all three, of the above three great classes of alimentary matters.

"But it is in the artificial food of man that we see this great principle of mixture most strongly exemplified. He, dissatisfied with the productions spontaneously furnished by nature, culls from every source, and, by the power of his reason, or rather his instinct, forms in every possible manner, and under every disguise, the same great alimentary compound. This, after all his cooking and art, how much soever he may be inclined to disbelieve it, is the sole object of his labour, and, the more nearly his results approach to this, the more nearly they approach perfection. Thus, from the earlier times, instinct has taught him to add oil or butter to farinaceous substances, such as bread, which are naturally defective in this principle. The same instinct has taught him to fatten animals, with the view of procuring the oleaginous in conjunction with the albuminous principle; which compound he finally consumes, for the most part in conjunction with saccharine principles, in the form of bread or vegetables. Even in the utmost refinements of his luxury, and in his choicest delicacies, the same great principle is attended to; and his sugar and flour, his eggs and butter, in all their various forms and combinations, are nothing more nor less than disguised imitations of the great alimentary prototype, *milk*, as presented to him by nature."

Appetite and satiety.—These sensations are in part taste itself, and in part sensations analogous to taste, like those which are excited by the food when appetite is wanting. The sense of appetite is heightened in winter and spring, by cold baths, by friction of the skin, by friction of the abdomen, and by the agitation to which the abdomen is subjected in horse exercise, as well as by muscular exertion.

Digestion excites in healthy persons a general feeling of satisfaction, with the sensation of warmth; but these feelings are not confined to the digestive organs, of which the principal sensitive nerve is the vagus, but extends to almost all the other parts of the body: it is probable, therefore, that it is in a great measure owing to excitement of the sympathetic nerves, which, as will be shown at a future page, possess in a high degree the faculty of transmitting impressions made on them.

Indigestion is a state of the digestive organs, in which either they do not secrete the fluid destined for the solution of the aliment, or they are in such a condition of irritability or atony, that by the mechanical irritation of the food painful sensations and irregular motions are excited. The local sensations of uneasiness in the digestive organs appear to have their seat principally in the nervus vagus, for any great irritation of that nerve in the œsophagus and pharynx seems to produce the same sensations of nausea as are the result of irritation of the stomach itself previous to vomiting. But the sympathetic affection of the whole nervous

system in such cases is not less striking, and seems to be likewise dependent on an impression made on the sympathetic nerve.

In *hunger* and *thirst* both kinds of sensations, the local and the general, are present, but the after phenomena are the direct effects of the want of nutriment and water in the system.

What is called *thirst* is, however, sometimes rather a call for the cooling influence of cold drinks, as, for instance, in the dry hot state of the air-passages, mouth, and skin produced in fevers by the increased temperature and diminished turgescence of the parts. Exhalation is in such cases often rather diminished, and the dryness of the surface arises from the circumstance that although blood still flows through the capillary vessels, the reciprocal action between the blood and the living tissues, which is denominated turgescence, or turgor vitalis, is depressed. No increased generation of caloric in the internal organs is required to account for the elevated heat of the skin, which arises from the absence of exhalation and of the cooling effect produced by the conversion of a fluid into a gaseous body.

The final consequences of unappeased thirst are a feverish state which does not apparently differ from that of nervous fevers, and with it inflammation of the air passages.

The local sensations of hunger, which are limited to the digestive organs, and appear to have their seat in the nervus vagus, are feelings of pressure, motion, contraction, qualmishness, with borborygmi, and finally pain. These sensations have been supposed to be caused by the saliva, by the bile, by the rubbing of the coats of the stomach against each other, or by the acrid gastric juice. Dumas imagines the feeling of hunger to arise from the action of the absorbent vessels of the alimentary canal being turned upon the coats of the stomach and intestines themselves. All these suppositions are quite inadmissible. The aliment is an "adequate," or "homogeneous" stimulus* to the digestive organs: when this stimulus is wanting, the state of the organ is made known to the sensorium by the nerves. The local sensations of hunger, as well as those of appetite and satiety, may, perhaps,—and Brachet† infers, from experiments which he has made, that they do,—cease to be felt after division of the nervus vagus; the sensation of hunger is put an end to, by the change which the assumption of food produces in the state of the gastric nerves, by strong impressions on the sensorium and the active states of it excited by passions or meditation, and by the change produced in the brain itself by taking opium, &c. The long fasting which insane persons are frequently observed to subject themselves to, may in like manner be accounted for, perhaps, by their having, in consequence of the morbid affection of their sensorium, lost the perception of the local sensation of hunger which incites us to take food.

* See pages 57 to 59.

† Recherches sur les fonctions du systême ganglionaire. Paris, 1830.

The general effects of long fasting, however, are observed to be for the most part similar even in different conditions of the digestive organs. They are feelings of general debility, actual and gradually increasing loss of strength, fever, delirium, violent passion, alternating with the deepest despondency. The temperature of the body is said to fall several degrees, though this is denied by Dr. Currie* to have been the case in a patient who died of inanition in consequence of stricture of the œsophagus. The respiration becomes fœtid, the urine acrid and burning, the lymphatic vessels, according to Magendie and Collard, bloody. Collard states that the quantity of their contents is increased when the animal has fasted only a short time, (?) and that it afterwards gradually decreases, but that even the lacteals still carry some little lymph about the middle period of the abstinence. Contraction of the stomach ensues. The secretions cease to be formed, although the gall-bladder is full, and bile still passes into the intestine. (It does not enter the stomach, according to Magendie.) The mucus of the mucous membranes becomes less abundant, as do all substances which can be absorbed. The pus from wounds, the milk, saliva, and the poison of serpents, cease to be secreted. The urine still contains urea; Lassaigne found that substance in the urine of a madman who had fasted eighteen days:† the urinary passages are not necessarily inflamed; the mucous membranes are pale. M. Collard states that the relative quantity of fibrin in the blood is diminished during fasting, while the proportion of solid matters due to the red particles is increased.‡ The stomach is found much contracted after death.

Experiments on the duration of life in man and animals deprived of food, show that warm-blooded animals are best able to support the want of food. The lower animals with a hard external skeleton will live an extraordinary length of time without food: I have been informed by letter that an African scorpion lived, during the voyage to Holland, and nine months after it arrived there and came into the possession of Dr. Dehaan, without taking any food. Rudolphi kept a proteus anguinus five years; Zoys had one ten years, living in spring water renewed from time to time, and having nothing else given to it. Salamanders, tortoises, and gold-fishes may likewise be kept for years without food, and it is well known that snakes will live for six months without eating. Redi found birds sustain the want of food for from five to twenty-eight days: a seal lived out of water, and without nourishment, for four weeks; dogs lived from twenty-five to thirty-six days without eating or drinking. Man does not generally support hunger and thirst longer than a week; hunger alone is borne much longer, especially in disease,

* On the effects of Water, cold and warm, as a remedy in fever. 1797.

† Journal de Chim. Med. 1825, Avr.

‡ Magendie's Journal de Physiol. t. viii. p. 171.

and still more in insanity.* The accounts of persons having lived without taking food for months and years are, as Rudolphi with justice remarked, examples of deception.†

CHAPTER II.

OF THE DIGESTIVE ORGANS.

a. Of the different forms of the alimentary canal.

It appears to be an universal character of animals that they have an internal cavity for the production of a chemical change in the aliment preparatory to assimilation—a cavity for digestion. This cavity is in most cases tubular, and open at its upper and lower extremity, but sometimes it is provided with but one, oral, opening; the remains of the food after digestion being expelled by the same opening by which it had been introduced.‡

The *infusoria* have been shown by the great discoveries of Ehrenberg to possess throughout the class a mouth surrounded with cilia; but this is not all; Ehrenberg has been enabled, by feeding the creatures with coloured substances, to distinguish the different forms of their digestive organs, and to found on these differences a division of the class into primary groups. Some he finds to have no intestine nor anus, but merely a single mouth, into which many cæcal stomachs open; this is the form of the digestive organs in the monads, &c. In others there is a complete intestinal canal furnished with mouth and anus, and communicating by narrow tubes with numerous cæcal stomachs; the intestine sometimes describes a circle in the body of the animal, terminating near the mouth in a ciliated ring at the upper extremity of the body, as in the vorticellæ; in other instances the mouth and anus are situated at opposite extremities of the animal; while, in others, again, the situation of the mouth and anus alternates, either one or other of them being at the extremity of the body; lastly, in another group, both mouth and anus open at the abdominal surface of the body. In loxodes cucullatus,—a polygastric animalcule with complete digestive canal,—Ehrenberg has discovered and described pharyngeal teeth.

In the *rotifera*, or *wheel animalcules*, there is an intestinal canal extending from the mouth to the anus, and in some Ehrenberg has discovered a dental apparatus. Most of them have two glandular-looking organs at the commencement of the intestinal tube.§

In the *acalepha* there is no anus nor intestinal tube; the aliment is

* See Tiedemann, Physiol. t. iii.

† All the subjects treated of in this chapter will be found more fully discussed in Tiedemann's work.

‡ On the Agastrica, see Meyen, Act. Nat. Cur. t. xvi. Suppl.

§ Ehrenberg, Physikal. Abhandl. der Königl. Akademie der Wissenschaften zu Berlin. 1830 und 1831.

conveyed by the mouth into a stomach which is ramified like a vascular system in the substance of the animal,—as in the medusæ; or the nutriment is taken up by the absorbent tubes of the tentacula, and by these carried to the stomach,—as in the rhizostomata; or, as appears to be the case in the berenice and others, the food, being taken up by absorbent tubes, is distributed through ramified digestive canals, there being no true stomach. And, even in cases where there is a stomach, ramifying tubes, like vessels, arise from it, and are distributed through the substance of the animal.

In the *polypifera*, of which some are free, others fixed, some simple, and others united on a common stem, the digestive organs are in some instances simple, consisting of a cæcal sac-like stomach, which is the form in the actiniæ, fungi, madrepora, tubipora, alcyonia, millepora, sertularia, and hydræ; in others, as in the alcyonellæ, there is a short intestinal canal, the anus opening near the mouth.*

In the *entozoa* the forms of the digestive cavity are exceedingly various. In the cystic worms the vesicular cavity of the body serves to fulfil the office of digestion; such, at least, seems to be the case in the cysticercus and cœnurus. In the cestoidea, or tape-worms, the intestine is described by Mehlis to commence as a simple tube, but to bifurcate very soon. In the trematoda, or suctorious worms, there is no anus, and the intestine is ramified through the body like a vessel, though there is besides,—for example, in the distoma,—a second system of vessels, which opens at the posterior part of the body, and which may perhaps communicate with the ramified intestinal canal by its smaller branches.† In the acanthocephala the anus is again wanting, and the bifurcate intestinal canal terminates by cæcal extremities. The nematoda, or round worms, have a simple tubular intestine provided with mouth and anus.

In the *planaria*, *prostoma*, *derostoma*, and other similar worms of fresh and salt water, so closely allied to the entozoa, particularly to the trematoda, there is again a marked systematic distinction in the forms of the digestive organs; the prostoma and derostoma having both mouth and anus, while in the planaria there is a ramified intestine, with the mouth at the abdominal surface of the body, but no distinct anus.‡

In the *radiata* there is sometimes,—as in the holothuria and echinoidea, &c.—an intestinal canal with both mouth and anus, which in the holothuria are at the opposite extremities of the body; while in the echinoidea the mouth is in the middle of the under surface, and the anus either in the middle of the upper surface,—as in the echinus,—or at the border of the shell,—as in the spatangus. In the asterioidea there is mere-

* See Hemprich and Ehrenberg, Symbolæ Physicæ. Berol. 1831. See also Meyen, Isis, 1828. Nov. Act. Nat. Cur. t. xv. Suppl.

† Mehlis de Distomate hepatico et lanceolato. Götting. 1825. Laurer, Disquis. Anatom. de Amphistomo conico. Gryphiæ, 1830.

‡ Ehrenberg, Symb. Physik.

ly a stomach with cæcal appendages, no intestinal canal nor anus; while in the crinoidea the intestine and anus are again met with,—as in the cornatula,—in which the anus is placed with the mouth at the under surface of the body.

In all the *annelida, crustacea, arachnida,* and *insecta,* there is an intestinal canal, with mouth and anus; but its form presents many varieties. We may mention, as particularly remarkable in these classes, the increase of digestive surface by means of cæca arising from the short intestinal tube in the phalangida, (a family or tribe of tracheary arachnida,) the dental apparatus in the stomach of crustacea,—for example, crabs and lobsters,—and of some insects (the orthoptera), and the complex form of the stomach in some carnivorous insects. In general, the alimentary canal of insects consists of an œsophagus, a crop, (which, however, is met with only in the hymenoptera, lepidoptera, and diptera,) the gizzard furnished on the inner surface with teeth or horny ridges, (which exists in the carnivorous coleoptera, and most orthoptera,) the chylific portion of the canal which extends to the insertion of the Malpighian, or so-called biliferous vessels, and the intestine which extends from that point to the anus.

In the *vertebrata* the stomach is usually a mere dilated portion of the alimentary tube. The intestine in *fishes* is usually short, but its want of length is sometimes compensated for by folds of the mucous membrane; in the rays and sharks, for example, the internal coat of the intestine forms a spiral valve extending from the stomach to the anus, which in fishes is generally situated in front of the opening of the urinary and genital organs.

In *birds* the stomach presents a complexity of structure which is not met with in fishes, amphibia, and reptiles. In addition to the crop, or sac-like diverticulum of the œsophagus,—an organ destined for the preparatory softening of the food, and pretty generally present in birds, being wanting only in the scansores, grallatores, natatores, insectivores, and cursores, or birds of the ostrich kind,—the stomach itself is divisible into two parts: 1. the so-called proventiculus, or glandular stomach, a dilatation of the cardia, in the walls of which there is an entire stratum of distinct glandular follicles; 2. the muscular stomach, or gizzard, which follows immediately upon the other. In carnivorous birds the walls of the gizzard are thinner, but they are very thick in those which feed on vegetable substances; and then the muscular coat forms two very thick lateral muscular masses, and the mucous membrane which lines their inner surface has a thick warty covering of epithelium. The large intestine is short and narrow, and has two cæca at its commencement, which are of greatest length in birds which feed on vegetable substances. The rectum, as in reptiles, opens into the cloaca, together with the urinary and genital organs.

In *mammalia*, the distinction between those feeding on vegetables and those which live on animal substances is of greatest interest. The glandular stomach of birds is not met with in the class mammalia as a distinct portion of the alimentary tube, the only structure analogous to it is presented by the accumulation of numerous glands about the cardia in some quadrupeds,—for instance, the beaver, phascolomys, &c.*

In several *rodent animals*, such as the hamster and water-rats, the stomach is already divided into two parts. In the great *kanguruh* it has three compartments; in the *sloth* even four; among the apes the *semnopitheci* have a compound stomach, consisting of three portions, the cardiac, with smooth simple parietes, a very wide sac-like portion, and a long tubular division like a large intestine. The complex structure of the stomach is, however, by no means an universal character of herbivorous mammalia, for, in the *solidungula*, (the horse, ass, &c.) the stomach is simple, its different regions being distinguished merely by the extension of the epithelium from the œsophagus over the cardiac portion. In the *pachydermata*, also, if we except the pecari and nilghau, in which the stomach has peculiar appendages, or sac-like dilatations, the organ is generally of simple structure. The stomach exhibits the most remarkable complexity of structure in the ruminants among herbivorous mammalia, and in the dolphins among those living on animal substances.

The last only of the four stomachs of the *ruminants* has the acid property which characterises the organ in other mammalia. The first three cavities have a distinct lining of epithelium, and may be regarded as divisions of the cardiac portion of the stomach, and destined for the softening of the vegetable food preparatory to true digestion. The first great compartment of the stomach, the *paunch*, is characterised by the numerous flattened papillæ of its inner surface; it effects little change in the food which is in it subjected to maceration by the saliva. The second smaller stomach, the *reticulum*, communicates freely with the paunch, and is distinguished by the honeycomb-like denticulated folds of its lining membrane. In the third stomach, the *manyplies* or *omasum*, the mucous membrane is thrown into numerous deep longitudinal folds, arranged side by side like the leaves of a book. The food having been softened in the first and second stomach, is after a certain time returned to the œsophagus and mouth, and having been a second time masticated, descends through the œsophagus into the third stomach, and passes thence by a narrow opening into the fourth, the *obomasum*, of which the mucous membrane is soft, and the form elongated almost like that of the intestine. The first and second stomachs may be regarded as diverticula from the cardiac portions of the œsophagus and stomach. The

* See Sir A. Home's Lectures on Comparative Anatomy, vol. ii. and Müller, de Gland. Secernentium penit. struct. tab. i. fig. 9, 10.

canal by which they communicate with the œsophagus can be closed and formed into a tube, so that the morsel of food is made to pass onwards directly into the third stomach without entering the first and second cavities.

In the *cetacea*, the complex structure of the stomach is met with both in the vegetable feeders and in those which live on animal substances. The stomach of the phytophagous manati has several compartments, and that of the zoophagous whales, also, has even five or more divisions.

The alimentary canal in the *carnivora* is generally much shorter than in the other orders, and the distinction between the small and large intestine is in them less marked, while in most herbivora the colon is very wide and very long. The *cæcum* also presents remarkable differences according to the kind of food which the animal takes. In general it is remarkably small in carnivora, while in the solidungula, ruminantia, and most rodentia, it is uncommonly long,—for example, in the horse it measures two and one-half feet; in the beaver, two feet.

The herbivorous mammalia afford examples of the *change from animal to vegetable food*, inasmuch as for a certain period after birth they are supported on the milk of the mother, and during that period the first stomach is small. But the changes which the alimentary canal of the tadpole undergoes is much more remarkable. The amphibia in the larva state have an intestinal canal of very great length, and appear at that time to feed principally on vegetable substances; at a later period the intestine is very short.

The most general inference to be deduced from the foregoing comparative review of the forms of the alimentary canal in the animal kingdom is, that vegetable substances require a much more extensive apparatus for their digestion than animal substances. The intimate connection which exists between the whole organisation of an animal and the nature of his food, has been set forth by Cuvier in so admirable a manner* that I cannot refrain from giving his own words. Cuvier says, "Every organised being forms a whole, an unique, and perfect system, the parts of which mutually correspond, and concur in the same definitive action by a reciprocal reaction. None of these parts can change without the whole changing; and, consequently, each of them, separately considered, points out and marks all the others. Thus, as I have before remarked, if the intestines of an animal are so organised as only to digest flesh, and that fresh, it follows that its jaws must be constructed to devour a prey, its claws to seize and tear it, its teeth to cut and divide it, the whole structure of the organs of motion such as to pursue and catch it, its perceptive organs to discern it at a distance; nature must even have placed in its brain the necessary instinct to know how to conceal

* Cuvier, Revolutions of the surface of the Globe. English translation, Whittaker, London, p. 59.

itself and lay snares for its victims. That the jaw may be enabled to seize, it must have a certain-shaped prominence for the articulation, a certain relation between the position of the resisting power and that of the strength employed with the fulcrum; a certain volume in the temporal muscle, requiring an equivalent extent in the hollow which receives it, and a certain convexity of the zygomatic arch under which it passes: this zygomatic arch must also possess a certain strength to give strength to the masseter muscle. That an animal may carry off his prey, a certain strength is requisite in the muscles which raise the head; whence results a determinate formation in the vertebræ or the muscles attached, and in the occiput where they are inserted. That the teeth may cut the flesh, they must be sharp; and they must be so more or less, according as they will have, more or less exclusively, flesh to cut. Their roots should be the more solid as they have more and larger bones to break. All these circumstances will in like manner influence the developement of all those parts which serve to move the jaw. That the claws may seize the prey, they must have a certain mobility in the talons, a certain strength in the nails, whence will result determinate formations in all the claws, and the necessary distribution of muscles and tendons; it will be necessary that the fore-arm have a certain facility of turning, whence again will result determinate formation in the bones which compose it; but the bone of the fore-arm articulating in the shoulder-bone, cannot change its structure without this latter also changes. In a word, the formation of the tooth bespeaks the structure of the articulation of the jaw; that of the scapula, that of the claws; just as the equation of a curve involves all its properties; and, in taking each property separately as the basis of a particular equation, we should find again both the ordinary equation and all the other certain properties; so the claw, the scapula, the articulation of the jaw, the thigh-bone, and all the other bones separately considered, require the certain tooth, or the tooth requires them reciprocally; and, beginning with any one, he who possessed a knowledge of the laws of organic economy would detect the whole animal. We see, for instance, very plainly, that hoofed animals must all be herbivorous, since they have no means of seizing upon their prey; we see, also, that having no other use for their fore-feet than to support their bodies, they have no occasion for so powerfully framed a shoulder; whence we may account for the absence of the clavicle and the acromion, and the straightness of the scapula: not having any occasion to turn the fore-leg, their radius will be solidly united to the ulna, or, at least, articulated by a hinge-joint, and not by ball and socket, with the humerus: their herbaceous diet will require teeth with a broad surface to crush seeds and herbs; this breadth must be irregular, and for this reason the enamel parts must alternate with the osseous parts; this sort of surface compelling horizon-

tal motion for grinding the food to pieces, the articulation of the jaw cannot form a hinge so close as in carnivorous animals; it must be flattened, and correspond with the facing of the temporal bones, more or less flattened; the temporal cavity, which will only contain a very small muscle, will be small and shallow," &c.

b. Of the membranes forming the coats of the alimentary canal.

The alimentary canal has an external serous investment derived from the peritoneum, a muscular coat lying under the serous coat, and a tunica propria, which forms a kind of fascia, or framework, on the outer surface of which the muscular fibres lie, while to its inner surface *the mucous membrane* is attached.*

The structure of the villi of the small intestine has been already described, and their relation to the process of lacteal absorption discussed.†

The glands of the mucous membrane of the small intestine remain to be considered. Three forms of these glands have been distinguished:

1. *The follicles of Lieberkuehn*—foramina, or depressions, so small as not to be visible without the aid of a glass, which are spread over the whole extent of the mucous membrane of the *small intestine*, and are in such number that when sufficiently magnified they give to the membrane the appearance of a sieve.‡ [To the same order of follicles, perhaps, belong the simple tubular follicles described by Dr. Boehm§ as occupying the whole extent of *the mucous membrane of the large intestine*, and which he represents as seen in a section of the membrane to be arranged perpendicularly side by side, their cæcal bases resting on the subjacent vascular membrane, (fig. 38, c,) while the spaces between their orifices, which are so minute as to be scarcely visible without the aid of a glass, are but little larger than the openings themselves. There are other follicles of the large intestine which are larger and much less numerous, and under the name of glandulæ solitariæ have been confounded with the duodenal glands of Brunner. Their form is that of a round simple

* In many fishes the mucous membrane of the œsophagus is continued into the air-bladder through the canal which leads from the one to the other. In many other fishes, however, no communication exists between the air-bladder and the pharynx, or œsophagus (see p. 314); and in these cases it appears extraordinary that the membrane lining the air-bladder, although mucous in its characters, should form a shut sac, which is contrary to the general law of mucous membranes. This apparent anomaly is explained, however, by the fact observed by V. Baer, (Froriep's Notizen, 848,) that the air-bladder is originally developed as a mere diverticulum, or process from the pharynx; consequently, in the fishes, in which it forms a closed sac, the communication between it and the pharynx must have existed originally, but has become obliterated.

† See page 267.

‡ They have been already described at page 270.

§ De Gland. Intestin. Struct. Penit. Berol. 1835.

cavity (fig. 38, A). They are most numerous in the cæcum and appendix. The *mucous membrane of the stomach* appears to have a structure similar to that described by Boehm as belonging to the large intestine.] It has been made the subject of examination by Dr. Sprott Boyd.† He describes it as having here and there a velvety appearance, from the presence of minute folds, or fold-like villi, but it is throughout characterised by small regular cells of the diameter of $\frac{1}{200}$th to $\frac{1}{350}$th of an inch; near the pylorus their diameter was $\frac{1}{100}$th of an inch. In the bottom of the cells (fig. 39, E) a number of minute openings were visible, and, on making a vertical section of the membrane, it was seen to be composed of perpendicular fibres, (fig. 39, F,) which Dr. Boyd believes to be tubes opening into the cells. In the pig he could distinguish the cavity of the tubes.

Fig. 38.*

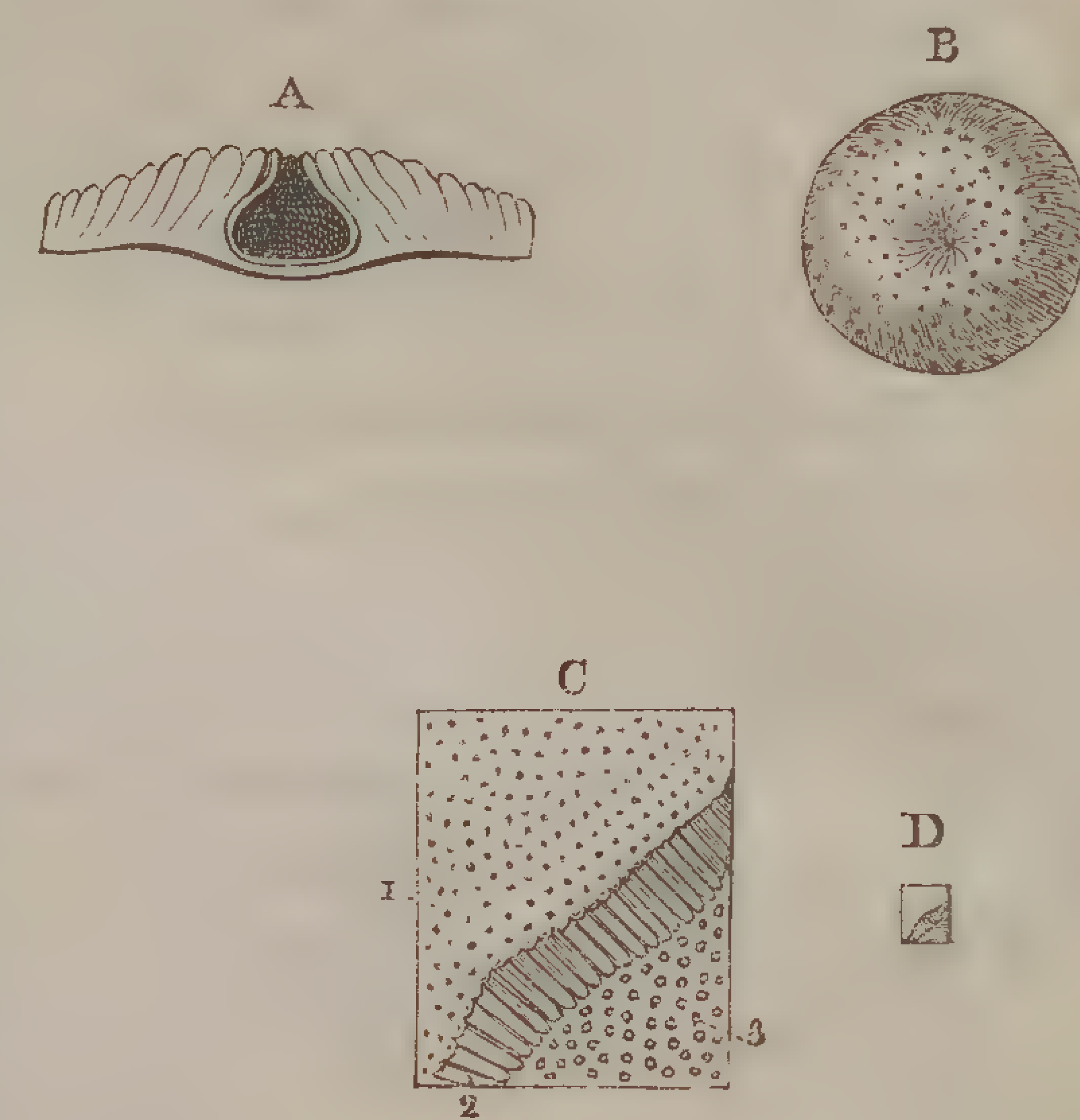
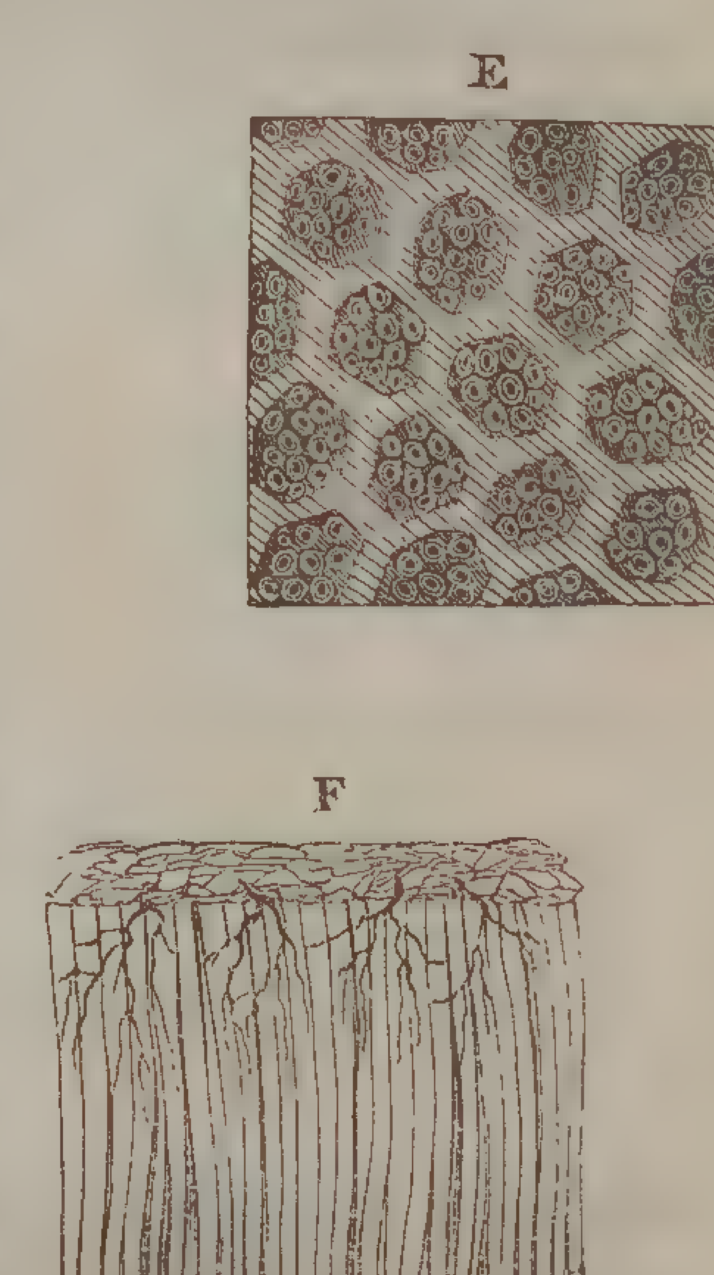


Fig. 39.‡



2. *Brunner's glands* — follicles visible to the naked eye, distributed singly in the membrane, and most numerous in the upper part of the small intestines.

[Very different structures have been confounded under the name of the glands of Brunner. Dr. Boehm has pointed out that the bodies described by Brunner, and regarded by

* [Follicles of the mucous membrane of the large intestine, from Dr. Boehm's paper just cited.—C. Enlarged view of the small tubular follicles which form the substance of the mucous membrane: 1. their openings seen on the surface; 2. the follicles, themselves, seen in a perpendicular section; 3. the surface of the cellular coat of the intestine, with pits for the closed extremities of the follicles:—D. natural size of the piece of membrane; A. section of one of the solitary follicles of the large intestine; B. the opening of the same, seen from above.]

† Inaugural Essay on the structure of the mucous membrane of the stomach, by Sprott Boyd. Edinb. 1836.

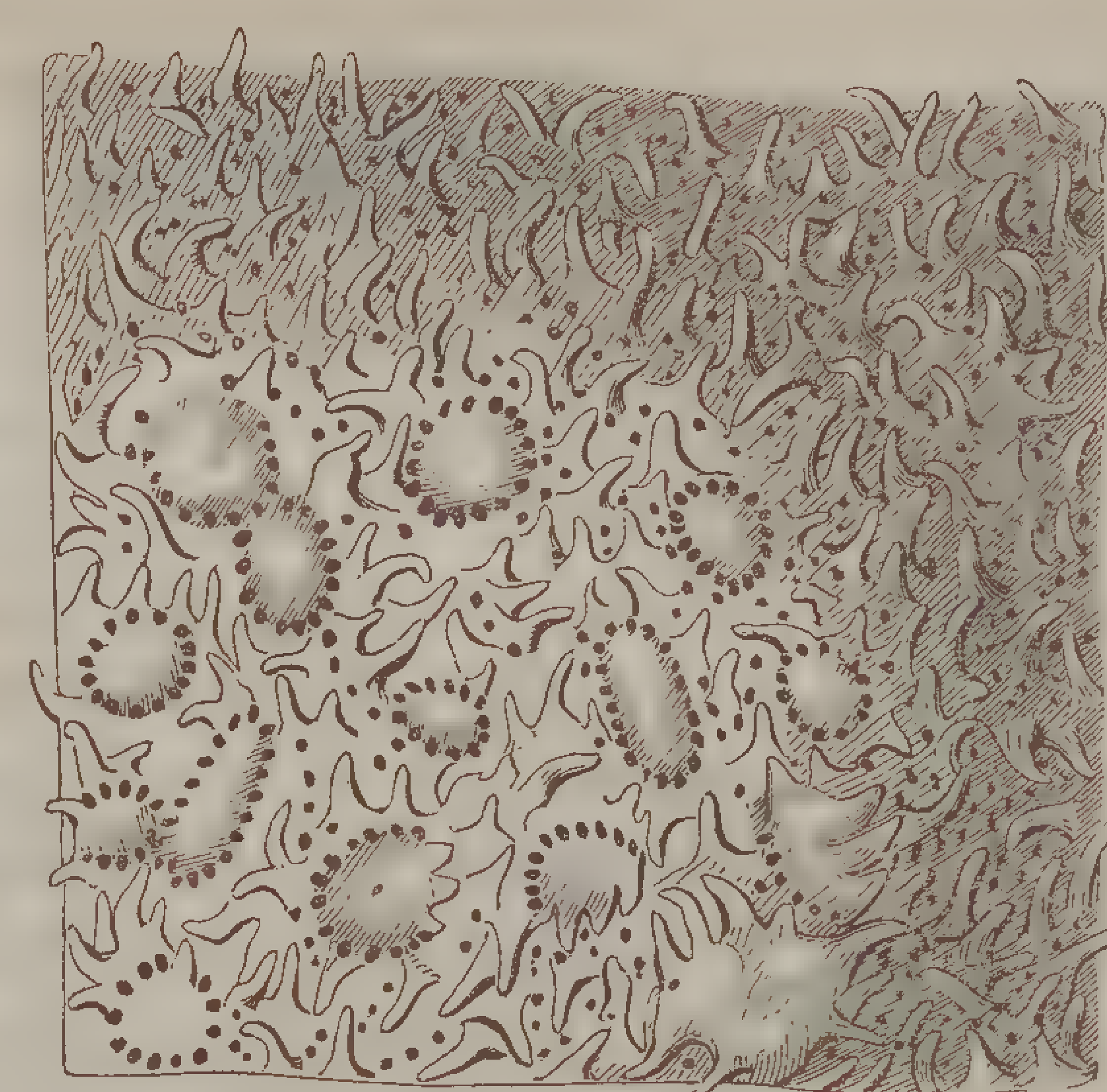
‡ [Mucous membrane of the stomach, from Dr. Boyd's paper.—E. Cells of human stomach,—open mouths of tube seen at the bottom of each,—magnified 32 diameters; F. section of mucous membrane of the stomach in the pig,—the cellular coat on which the bases of the tubes rest has been injected,—magnified about 20 diameters.]

him as analogous to the pancreas, do not exist lower down in the intestinal canal than the end of the duodenum, or commencement of the jejunum. They are little solid glands formed of several minute lobules, lying under the mucous membrane, and, by their great number near the pylorus, constituting there a continuous layer in the coats of the intestine.]

3. The so-called *glandulæ agminatæ*, or *glands of Peyer*,—which have their seat along the side of the intestine opposed to the insertion of the mesentery. The nature of these thickened, generally oval patches of the mucous membrane, has, up to the present time, been quite unknown; Rudolphi's treatise informed us of their more general external characters only. They have recently acquired increased importance on account of their undergoing certain morbid changes, suppuration and ulceration, in the typhoid fever attended with affection of the bowels; and it has become most desirable to have a more accurate knowledge of their structure, in order to know the real seat and nature of those morbid changes. The following account of them is the result of Dr. Boehm's researches, and I may remark that I have verified his observations. For the examination of the glands of Peyer, the intestine of healthy persons must be selected; the intestine of those who have died suddenly is therefore to be preferred. In many chronic diseases, particularly when they affect the intestinal canal itself, the organs in question become very much altered, and, if examined in that state, a false idea of their structure is obtained. Whenever they present the appearance of shallow cells arranged side by side, they are not in a healthy state, for their form has naturally no analogy with open cells or follicles. If one of the patches of Peyer's glands is examined with the microscope in a healthy intestine, after the surface has been gently washed, and the gland itself cleansed by means of a soft camel's hair pencil, it is readily seen that the thicker aspect of the membrane in these patches is in part owing to the size and number of the villi, which are here broader than in other parts, particularly at their root. The mucous membrane between the villi presents here, as in other parts of the intestine, the numerous follicles of Lieberkuehn; but in addition to these there are seen circular white spots, about one line in diameter, in which the mucous membrane is generally free from villi: in very few there are traces of very short villi. In the human subject these spots are only slightly raised; it is very seldom that the centre of the spot forms a short pyramidal white point. In other animals, particularly in the dog, cat, and rabbit, they are more elevated, and in the dog look like white papillæ; in the cat and rabbit they are surrounded by a circular furrow, and have themselves a flattened surface, so as to resemble the papillæ vallatæ of the tongue. Each of the white spots, of which several are contained in each patch of the glands of Peyer, is surrounded by a zone

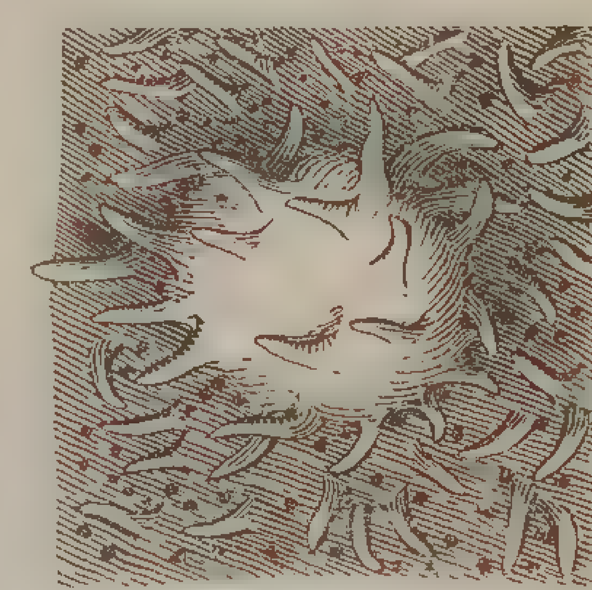
of openings like those of Lieberkuehn's follicles, (see fig. 40,) except that they are more elongated; and the direction of the long diameter of each opening is such that the whole produce a radiated appearance around the white spot. The number of openings in each zone is about ten, and they are generally arranged in a circular manner. No opening is visible in the surface of the white spot, except in birds; in them there is a small opening. (In my work on the glands, I mentioned and gave a representation of the appearance of Peyer's glands, which we have here described after Boehm; I had noticed it only in the cat.) Dr. Boehm tried in vain, both in the human subject and other animals, to express any secretion from the white bodies through an external opening, as he would have been able to have done if they were follicles; nor did pressure force the contents of the white bodies out through the openings which form a zone around each of them. On rupturing the surface of one of the bodies, a cavity is opened which corresponds in extent to that of the white spot previously seen, and is of considerable depth, though less deep than broad. The contents of the cavity are a greyish-white mucous matter, containing granules smaller than the ordinary particles of mucus. The membrane which covers in the cavity is extremely thin. It appears then that there are no large follicles with open mouths or cells in the patches of the so-called "Peyer's glands," but merely sacculi, of which the nature is unknown. The appearance of cells or follicles is not produced until the delicate membrane which shuts in these sacs is destroyed, which is so frequently the result of disease in these organs. [The solitary glands of the lower part of the small intestines, which have been confounded with the glands of Brunner, are, according to Boehm, single sacculi, similar to those which, when aggregated, form the patches of Peyer; they are also surrounded with a zone of openings, contain a white matter, and become diseased, in the same cases as the aggregated sacculi, but they are beset with villi. (fig. 41.)]

Fig. 40.*



* [Part of a patch of the so-called Peyer's glands magnified, showing the various forms of the sacculi, with their zone of foramina. The rest of the membrane marked with Lieberkuehn's follicles and sprinkled with villi. After Boehm, loc. cit.]

Fig. 41.*



The *third coat* of the digestive organs is formed by the contractile, fibrous, or muscular layer which is continued from the pharynx to the anus, and sends prolongations on the efferent ducts of the glands which open into the canal.

The *serous coat* belongs only to that part of the canal which lies within the abdominal cavity. The intestinal tube, as well as the liver and spleen, are thrust, as it were, into the peritoneal sac, carrying before them a part of the membrane which forms an investment for each, while the parts of the membrane kept asunder by the organ, which thus folds the sac in upon itself, meet at its posterior border, and are applied to each other so as to form a mesentery, or suspensory ligament. Nearly the whole of the intestinal canal, with the exception of the duodenum, has a mesentery or suspensory band of this kind. I have pointed out† that in the earliest stage of embryonic life the stomach likewise has a band of this kind, (a mesogastrium,) which at a later period undergoes a remarkable change, being converted into a sac, the great omentum; but it is not till the third or fourth month of fœtal life that the great omentum and transverse mesocolon become continuous in consequence of the mesogastric fold, which has now formed the omental sac, being pushed downwards, as it were, still farther, till the colon and mesocolon are brought to form part of the great omental sac, and are connected with the stomach in a manner which appears inexplicable before its mode of production is known. In many mammalia, —as the dog, cat, hedgehog, rabbit, and horse,—this connection between the stomach and colon does not exist, the great omentum or mesogastrium in them passing backwards to be attached to the vertebral column without being connected with the mesocolon, which arises from the vertebral column quite separately. The same is the condition in the human embryo in the earlier stages of fœtal life.‡

* [Solitary gland, or sacculus, of small intestine. After Boehm.]

† Meckel's Archiv. 1830, page 395.

‡ In the commencement of embryonic life, and indeed up to the fourth or fifth week, the position of the stomach is nearly vertical; the lesser curvature being turned to the right, the greater curvature towards the left side, and the pylorus directed downwards. The band by which the stomach is then attached to the posterior wall of the abdomen is a fold, likewise perpendicular, which arises from the middle line of the vertebral column, and extends towards the left side, to be attached to the great curvature of the stomach; its two layers investing the anterior and posterior walls of the stomach, and meeting again at the upper part of the smaller curvature, form a fold which is continued thence to the liver.

Now, from the circumstance of the mesogastrium arising from the vertebral column in the middle line, and thence extending to the left side to reach the great curvature of the stomach, a crescent-shaped sac is produced behind the stomach and in front of the mesogastrium, the opening into this sac being at the lower part of the lesser cur-

The omentum can perform no very important part in the function of the digestive organs, since in many animals it has not the same anatomical connections, and is represented merely by a loose band extending from the stomach.

CHAPTER III.

OF THE MOVEMENTS OF THE ALIMENTARY CANAL.

THE muscular coat of the alimentary tube is one of that series of contractile organs of which the motion is involuntary, and dependent on the sympathetic nerve. The cerebro-spinal nervous system has but a li-

vature, just below the fold above mentioned, which connects the stomach to the transverse fissure of the liver; this opening, which is at first very large, is at a later period called the foramen ovale.

The cavity behind the stomach preserves its form, but the opening into it on the right side becomes smaller, in proportion as the fold, extending from the lesser curvature of the stomach to the liver, descends, and the pylorus rises towards the liver, the stomach itself assuming an oblique direction. While the change in the direction of the stomach is going on, the greater curvature becoming more inferior, and the lesser curvature superior, the insertion of the mesogastrium into the posterior wall of the abdomen, which had till then been perpendicular and in the middle line, takes a more oblique direction towards the left side; and at the same time the sac formed by the mesogastrium, where it passes forwards to the great curvature of the stomach, becomes prolonged downwards, and the prolonged portion of the sac assumes a wrinkled appearance. The cavity enclosed behind the stomach in the sac of the mesogastrium and great omentum, is at first entirely to the right side of the perpendicular mesogastric fold; but it now, when the position of the stomach is changed, extends more to the left side, and in the transverse direction, constituting the lesser sac of the peritoneum.

The mesogastrium, or great omentum, and the transverse mesocolon, are as yet quite distinct and unconnected, except through the medium of the peritoneum covering the posterior wall of the abdomen, from which both arise. But in proportion as the colon assumes its arched position and approaches the stomach, while the peritoneal sac of the great omentum or mesogastrium is elongated, and its oblique insertion into the posterior wall of the abdominal cavity shifted downwards, the attachment of the mesogastrium, or great omentum, to the posterior wall of the abdomen, and that of the transverse mesocolon, approach each other, the portion of peritoneum between them being taken up to form part of the external lamella of the omental sac, till at last it is entirely lost. This change proceeds from the right to the left side, the insertion of the mesogastrium being oblique in direction, and higher up on the left side.

The process by which the insertions of the omentum and transverse mesocolon become confounded together, was first noticed by Meckel: I have confirmed his observation. The omentum appears to apply itself, at length, to the posterior surface of the transverse colon itself; the internal layer of the omentum then extends over the upper surface of the colon, forms the upper lamina of the transverse mesocolon, and thus reaches the posterior wall of the abdomen, and the external layer of the great omentum, which descends from the anterior surface of the stomach, then appears to invest the under surface of the transverse colon, and form the inferior lamina of the transverse mesocolon, but it in fact reaches only to the colon itself; the inferior lamina of the transverse mesocolon is the same portion of membrane which originally formed that part before the insertions of the mesogastrium and mesocolon became one.

mited influence over it; but this influence is evidenced by manifold sympathies which are observed to exist between the digestive apparatus and the brain and spinal marrow.

The commencement and termination only of the canal have muscles which are subject to cerebro-spinal nerves and the will; such as the muscles of the mouth, and the muscles moving the lower jaw and pharynx, on the one hand, and on the other the muscles about the anus.

The motions of the pharynx are under the command of the will, those of the œsophagus are not; although both are supplied by the nervus vagus. This apparently extraordinary circumstance may be explained in two ways: either, first, by supposing that the lower part of the nervus vagus, which forms the œsophageal plexus, loses its voluntary power in consequence of receiving branches from the sympathetic nerve; or, secondly, by admitting the hypothesis of Scarpa, Arnold, and Bischoff,* viz. that the vagus is itself a nerve of sensation, and that it is to its junction with the nervus accessorius that its motor branches owe their power of exciting motion; that the pharyngeal and laryngeal branches of the vagus in fact contain fibrils from the nervus accessorius, while the lower part of the vagus has no fibres of this nerve, and possesses therefore no motor power. The latter theory agrees very well with the fact observed by Magendie and myself, that stimulants applied to the vagus excite not the slightest motion of the stomach. Tiedemann and Gmelin state that they have excited contractions of the stomach by mechanical irritation of the vagus; but I have repeated the experiment on mammalia—rabbits and dogs—and on birds, so often, that I cannot but believe that there was some error in their observation. Which of the above hypotheses is correct, cannot, however, be at present determined. Further observations on the function of the nervus vagus will be found in the third book on the nervous system.

I consider it unnecessary to explain the movements of sucking, the prehension of food, and mastication.† The internal causes of such instinctive motions as the *sucking of new-born children* must remain enigmatical. It is difficult in this case to remain satisfied with Cuvier's theory of "instinct;" viz. that animals still so young are impelled to these actions by a dream of images, which, independently of their will, is being constantly called up in their brain,—by an innate idea, as it were, which arises out of their organisation or their necessities, just as the equation of a curve involves in it all the properties of the curve. We may, however, for the present content ourselves with supposing that in the sensorium of the infant there exists an irresistible impulse to the production, when possible, of the motions of sucking; and in accordance with this we find that infants suck even their own lips: and Mayer has observed

* Nervi accessorii Anatomia et Physiologia. Heidelb.

† On these movements, see Treviranus, Biologie, t. iv.

that after the head of young animals has been separated from the trunk, a finger introduced between the lips is seized.

We shall now treat more at length of the movements of deglutition, and the movements of the stomach—rumination, vomiting, and eructation,—the movements of the intestines, and the expulsion of the fæces.

1. *Deglutition.*—In deglutition there are three acts: in the first the parts of the food collected to a morsel glide between the surface of the tongue and the palatine arch till they have passed the anterior arch of the fauces; in the second act the morsel is carried past the constrictors of the pharynx; in the third it reaches the stomach through the œsophagus. These three acts follow each other with extreme rapidity: the first is performed voluntarily by the muscles of the tongue, under the influence of the hypoglossal and glosso-pharyngeal nerves. The second also is effected with the aid of muscles which are in part endued with voluntary motion, such as the superior and inferior muscles of the soft palate; but it is nevertheless an involuntary act, for it takes place without our being able to prevent it, as soon as a morsel of food, drink, or saliva is carried backwards to a certain point of the tongue's surface. The third act is executed, independently of the will, by muscles, of which the contractions are always involuntary.

The second act of deglutition is a very complicated process, concerning which there is a difference of opinion among writers. To understand it rightly, it is above all things necessary to have a correct notion of the position of the palatine arches in the different stages of the act. The anterior arch, formed by the palato-glossal muscles, constitutes with the tongue a constrictor muscle, and has been correctly termed the constrictor isthmi faucium. The posterior arch, formed by the palato-pharyngeal muscles, has the same action when its superior and inferior points of attachment are fixed. But when the soft palate is fixed by the action of the tensores palati, and the lower attachments of the posterior palatine arch are approximated to each other by the contraction of the pharynx, the palato-pharyngeal muscles themselves contracting must cause the sides of the arch which they form to approach each other like curtains from the sides, so as to reduce the passage between them to a mere chink, which is larger below than above. Now, Dzondi* has proved that this approximation of the sides of the posterior palatine arch takes place in deglutition to such a degree that they nearly come into contact; and we may convince ourselves of the fact by examining the parts with one finger while we execute the movement of deglutition, or by viewing the fauces in a mirror, pressing down the tongue at the time, while we swallow. We then perceive that, during the motions which we have described, the parts form an inclined plane, which is directed obliquely backwards and downwards, and prevents the food

* Die Functionen des weichen Gaumens. Halle, 1831.

from passing into the upper part of the pharynx and the posterior nares. The uvula during the movement is relaxed, and is applied to the cleft between the approximated sides of the arch. I have repeated the experiment, and observed what Dzondi describes. Most writers, M. Magendie even, incorrectly state that during deglutition the food is prevented from entering the posterior nares by the soft palate being raised; a movement which, if performed, could not in any case completely cut off the pharynx from the posterior nares. Whenever the communication between the nasal canal and the pharynx is closed, this is effected by the approximation of the sides of the posterior palatine arch, or velum palati posterius, as Dzondi calls it.

The mechanism of deglutition is, then, according to Dzondi, as follows. In the first act the morsel is carried backwards by being pressed between the tongue and palate till it has passed the anterior palatine arch.

In the second act the further motion of the food is effected by the tongue being carried backwards, and by the muscles of the anterior palatine arch contracting behind the morsel, the direction of its motion being determined by the state of the walls of the fauces at the time. By the root of the tongue being retracted, and by the larynx being raised and carried forwards under it, the epiglottis is pressed over the rima glottidis, and the morsel glides past it without danger. At the same time the approximation of the sides of the posterior palatine arch, as described above, cuts off the passage into the upper part of the pharynx and the posterior nares, and the morsel slides over the surface of the inclined plane into the pharynx, which is brought up to receive it, and which, now contracting, forces it onwards into the œsophagus. During the act here described, the tongue, the muscles of the anterior and posterior palatine arches, the superior muscles of the soft palate, (which they make tense and fix,) and the constrictors of the pharynx, are all in action: the soft palate itself is neither depressed nor carried backwards towards the posterior nares; it is merely made tense and a little raised.*

In the third act, in which the food passes through the œsophagus, every part of that tube, as it receives the morsel, and is dilated by it, is stimulated to contract: the undulating contraction of the œsophagus, which is particularly observable in horses while drinking, proceeds very rapidly along the tube; it is only when the morsels swallowed are large, or taken too quickly in succession, that the progressive contraction of the œsophagus is slow, and attended with pain. The morsel of food and the drink are at each point of their transit included in contractile walls, which are closely applied to them. In articulo mortis, when the œsophagus is already paralysed, this action is not performed, and drink is heard to run down with a rattling sound.

* See Dzondi, loc. cit. Tab. iv.

The third act of deglutition is perfectly involuntary, being performed by the muscular fibres of the œsophagus, which are not in the slightest degree capable of voluntary motion. The muscles which perform the second act, viz. the muscles of the tongue and pharynx, are, on the contrary, capable of executing voluntary movements; and indeed, if the fauces are moist, although there be no morsel to swallow, deglutition can be performed voluntarily, although not many times in succession. A part of the motion of the second act of deglutition, as the approximation of the sides of the posterior palatine arch, may also be performed voluntarily, without the whole process of deglutition necessarily following. By means of a mirror we may convince ourselves that we have some voluntary influence over the muscles of the fauces and pharynx, independently of deglutition. But if several of these movements, for instance, that of the tongue and that of the posterior palatine arch, are excited, either voluntarily or by the contact of a stimulus, the action of the whole group of muscles belonging to deglutition, with the constrictors of the pharynx also, ensues, and any portion of food, drink, or saliva, which has passed beyond a certain limit in the mouth, is swallowed without our being able to prevent it.

In the *true serpents*, in which the superior maxillary bones can be in some measure separated from each other like the two halves of the inferior maxilla, and in which, by means of the long ossa quadrata extending from the moveable temporal bones to the lower jaw, the throat is capable of great dilatation, the act of swallowing consists, as Rudolphi aptly remarks, in the organs of deglutition being drawn over the bulky prey.

Influence of the epiglottis in deglutition.—M. Magendie* has confirmed the observation made originally by Galen that the rima glottidis itself is closed during deglutition. But he has gone too far in admitting that removal of the epiglottis does not prevent deglutition being performed. Even allowing this conclusion, which M. Magendie has deduced from experiments on animals, to be correct, it is equally certain, as the numerous records of cases in which the epiglottis had been lost by ulceration of the larynx, and Reichel's experiments,† show, that the movements of deglutition are thereby impeded.‡

In cetaceous animals, the upper portion of the larynx, which in these animals is bill-shaped, is drawn up towards the nasal cavities during swallowing; and the food, pressed backwards by the tongue, passes by its side into the pharynx. No animals but mammalia have a velum palati, and, with few exceptions, an epiglottis.

2. *Movements of the œsophagus.*—M. Magendie has observed the sin-

* Mémoires sur l'usage de l'Epiglotte dans la Déglutition. Paris, 1813.

† De usu Epiglottidis. Berol. 1816.

‡ On this subject, consult Rudolphi's Physiologie, ii. 378; and Lund, Vivisectionen; Kopenhagen, 1825; p. 9.

gular fact of the occurrence of rhythmic contractions of the lower part of the œsophagus independently of deglutition. I have myself since seen these contractions; they proceed downwards with great rapidity towards the cardiac orifice of the stomach, and continue about thirty seconds: according to M. Magendie, their duration is longer in proportion to the fulness of the stomach at the time, being sometimes as much as ten minutes. The contraction, according to my observation, passes gradually into a state of relaxation, which is again succeeded by contraction. While the œsophagus was contracted, M. Magendie was unable to force any of the contents of the stomach into it; but, during its relaxed state, fluids escaped into the œsophagus from the stomach by the force of gravity alone, and were either expelled by the mouth,—which, however, happened rarely, —or—which was usually the case—they were repelled into the stomach by the renewed contraction of the œsophagus. It is evident, therefore, that the cardiac orifice cannot be regarded as at all times strongly closed; it is probable that the relaxation of the œsophagus is more frequent in dyspepsia, and, if so, it will be easy to explain the occurrence of eructation — the rising of air and food into the mouth—in persons labouring under it, whether we attribute the escape of the ingesta from the stomach to contractions of that viscus at the moment of the relaxation of the œsophagus, or to diminution of the capacity of the abdominal cavity consequent on the contraction of the diaphragm.

The experiments of Magendie, Legallois, and Beclard, have demonstrated that in the act of vomiting the œsophagus performs an anti-peristaltic motion, the reverse of that which it executes in deglutition. When vomiting had been produced by the injection of tartar emetic into the veins, the anti-peristaltic motions of the œsophagus still continued, even though it had been separated from the stomach.*

3. *Movements of the stomach during digestion.*—The contractions of the strong muscular gizzard of the granivorous birds must be very forcible, and the stomach of many crustacea, and of orthopterous insects, has certainly a mechanical action; but the motions of the membranous stomach of other animals, and of man, appear to be in the healthy state very feeble. When we open animals still living, we always observe, it is true, that the stomach embraces tightly its contents, but yet it presents a most striking contrast to the incessant peristaltic motions of the intestines, which are especially active under the stimulus of the air.

Neither irritation of the nervus vagus in rabbits, dogs, and carnivorous birds, nor irritation of the cœliac ganglion in the rabbit, appears to exert the slightest influence on the stomach. The irritation must be applied to the stomach itself, and it then produces immediate contraction.

* Lund, loc. cit. p. 15.

It is evident, then, that those writers must greatly err who ascribe much importance to the motions of the stomach in effecting the division of the food. I have never seen the peristaltic motions of the stomach distinctly; I shall therefore give M. Magendie's description of them.*

The stomach in the first period of digestion is uniformly distended, but the whole extent of the pyloric portion afterwards contracts; the chyme into which the food is converted collects in the pyloric portion, while the portion of food which has been less acted on remains in the splenic extremity of the stomach. The peristaltic motions, which are stated by M. Magendie to continue even after the nervi vagi have been divided, are described as follows: After the stomach has been for some time motionless, the commencement of the duodenum contracts, then the pylorus, and the pyloric portion of the stomach, by which means the chyme is pressed towards the splenic portion. The stomach then becomes distended anew, and its pyloric portion now contracts from left to right, impelling the chyme towards the duodenum, and as much of the food as has undergone the necessary solution in the stomach passes through the pylorus into the intestines. These motions are repeated several times, then cease, to be renewed after a certain interval. While the stomach is full, the motions are limited to the region of the pylorus; but, in proportion as it empties itself, the motions become more extended, and, when the organ is nearly empty, they are seen even in the splenic portion.

Schultz† imagines that in animals, such as the rabbit and horse, in which the stomach has a dilated fundus, the motions of the stomach are such as to cause the food to describe a circle along the two curvatures; while in the carnivora, in which the fundus or splenic extremity is less dilated, the food is thrown backwards and forwards to and from the pylorus; and hence it is, he supposes, that the former animals vomit with difficulty, the latter more readily.

The motions of the stomach have been observed by Dr. Beaumont in a man who, in consequence of a gun-shot wound, had a considerable opening in the stomach, the margins of which had united with the borders of the wound in the abdominal parietes.‡

He found that, when digestion was not going on, the stomach was contracted; that the food, as soon as it entered the stomach, was moved from the fundus along the great curvature from left to right, and then along the lesser curvature from right to left. He perceived the effect

* Préc. élément. de Physiol. 2nd edit. t. ii. p. 87. Dr. Milligan's Translation, 4th edit. p. 286.

† De Alimentorum Concoctione. Berol. 1834.

‡ Experiments and Observations on the Gastric Juice, and the physiology of Digestion, by W. Beaumont. Boston, U. S 1834.

of the same motions in the changes of position which the bulb of a thermometer introduced into the stomach underwent. These circular motions occupied from one to three minutes. They increased in rapidity as the process of chymification advanced.

Dr. Beaumont observed, likewise, that the commencement of the conical part of the stomach, about three inches from the small extremity, was the seat of peculiar contractions and relaxations. The bulb of the thermometer, when placed at that point, was tightly embraced from time to time, and retracted towards the pylorus for a distance of three or four inches.

During the first period of digestion the pyloric orifice seems to be quite closed. Its contraction is, according to Wepfer, and Tiedemann and Gmelin, sometimes so strong, that, even when the stomach is separated from the intestines, none of its contents escape. Mr. Abernethy, too, states that in the human subject fluids do not at first pass at all readily through the pylorus: in the case of a person who had been poisoned with opium, and into whose stomach a large quantity of fluid had been injected during life, all the fluid was found still in the stomach after death. M. Magendie believes that the greater part of the fluid taken into the stomach is absorbed directly from it; nevertheless he remarks that in the horse the water taken into the stomach passes quickly through the pylorus, and so finds its way as far as the capacious cæcum, and that even the food escapes in part through the pylorus. Mr. Coleman gave a horse to drink, and after the lapse of six minutes the water was found to have passed through the pylorus and small intestines, even as far as the cæcum.*

Towards the termination of the digestive process the pylorus seems to offer a more feeble resistance to the passage of substances from the stomach, for it is known to allow the transit even of undigested substances, such as cherry-stones, and other larger bodies. The central constriction of which the stomach was by Sir E. Home imagined to be the seat during digestion, has never been really observed. Neither Tiedemann nor I have seen anything of the kind in dogs.

4. *Rumination.*—In ruminating animals the œsophagus opens immediately into the first and second stomachs, but it is continued onwards to the third stomach in the form of a groove, or half canal, with thick lips. It appears from the observations of Flourens† on the sheep, that the food, whether it consist of grass, oats, or turnips, first passes into the first and second stomachs simultaneously. A finely divided substance—as a mash of chewed turnips—was given to a sheep, and it was found to pass into the first and second stomach, while a small portion reached the third. The food, softened by the action of the

* Abernethy's Physiological Lectures, 180.

† Revue Encyclopédique; Paris, Nov. 1831; p. 542.

saliva, and the secretions of the first and second stomachs, is returned from them by a movement like that of eructation to the mouth, and, after being a second time chewed, is again swallowed. With the view of discovering what takes place in this second deglutition, Flourens made an artificial opening into the different stomachs in different animals; he kept the openings closed except when he wished to observe what was going forward within. By this procedure he found that, when the food is swallowed the second time, a part of it still passes into the paunch and reticulum, but that a large portion follows the œsophageal groove or canal into the third stomach. Flourens offers the following explanation of the different course taken by the food before and after rumination. When first swallowed, the morsels, he says, are large, and dilate the œsophagus at the cost of the groove leading from it to the third stomach, and therefore necessarily enter the paunch. After rumination, however, the food is soft, and, without dilating the œsophagus, follows the groove which leads to the third stomach, although a small portion may still enter the first. If the rhythmic contractions of the lower part of the œsophagus during digestion, observed by M. Magendie and myself in other animals, take place likewise in ruminants, they would cause the lips of the groove leading to the third stomach to meet so as to form an entire canal, through which food finely divided by rumination would pass, though the large morsels of food, when first swallowed, would dilate it.*

With respect to vomiting in the ruminantia, Flourens found that, while the first two stomachs have the power of returning the food to the mouth for rumination, the fourth stomach, by which the act of vomiting is performed, is with very great difficulty excited to execute the necessary movement.

5. *Vomiting.*—Vomiting is an anti-peristaltic motion of the stomach and œsophagus, sometimes of a part of the intestines likewise, attended with nausea, and accompanied by violent contractions of the abdominal muscles and diaphragm; it is excited by any violent irritation of the pharynx, œsophagus, stomach, or intestine, whether it acts immediately on these parts, or through the medium of the nerves going to them; and it takes place also when substances capable of irritating the organs which we have named are introduced into the circulation from other parts of the system. Thus vomiting is excited by mechanical irritation of the pharynx by means of a feather, or the finger, or even by a morsel of food retained too long at that part; by all substances which irritate the stomach either mechanically or chemically; by inflammation of the stomach or intestinal canal; by the strangulation of herniæ, or intus-susception of a portion of intestine; by irritation of the brain, or interruption of the cerebral influence in consequence of division or ligature of

* See Berthold, Beiträge zur Anat. Zoot. u. Physiol. Gött. 1831.

the vagi nerves; sometimes, indeed, it is produced by the movements accompanying coughing; lastly, by injuries to the head, and the injection of tartar emetic into the veins. All substances which, when their action is moderate, promote the peristaltic motions of the irritated parts, by a more violent operation cause the motions to become reversed, and by nervous sympathy excite other parts not previously acted on to concur in the production of vomiting. The state of the posterior palatine arch is stated by Dzondi to be the same during vomiting as in deglutition, with the exception that the inclined plane formed by the approximation of the sides of the arch to each other is more raised, and that the uvula is shortened by the action of its muscles. This arrangement of the parts directs the matters vomited into the mouth, and prevents their entering the nostrils; although, on account of the sides of the posterior arches, even when drawn together, not meeting accurately at the lower part, a passage is left from the pharynx to the posterior nares, and matters vomited are therefore sometimes thrown into the latter cavities. Carnivorous animals vomit readily, the horse with great difficulty.

Action of the stomach in vomiting.—The opinion that the stomach itself has no share in the act of vomiting had been already advanced by Bayle, Chirac, Lenac, and John Hunter, but was refuted by Haller; it has been again revived by M. Magendie, who maintains that the stomach is itself quite passive during vomiting, and that the expulsion of its contents is effected solely by the pressure exerted upon it when the capacity of the abdomen is diminished by the contraction of the diaphragm and abdominal muscles. M. Magendie injected tartar emetic into the veins of dogs, and in other instances gave it by the mouth, but he never saw the stomach itself contract; and if in such cases he drew the stomach out of the abdominal cavity, vomiting was prevented, until he returned the viscus to its natural situation, when vomiting immediately ensued. Pressure with the hand had the same influence as the abdominal muscles; and even the action of the diaphragm alone pressing against the linea alba was sufficient to produce vomiting when the abdominal muscles had been cut away. Division of the phrenic nerve put a stop to the vomiting. M. Magendie states, that, when the stomach was removed, and a pig's bladder connected with the œsophagus in its stead, vomiting took place just as when the stomach itself remained uninjured.

M. Magendie's conclusions were controverted, however, by M. Maingault, who stated that he has seen vomiting occur when both the diaphragm and abdominal muscles had been divided. This gave rise to further investigation, and the committee appointed by the Academy of Paris found, that without external pressure on the stomach vomiting could not take place, but that this pressure need only be very slight; for that, after the abdominal muscles had been divided, and the diaphragm paralysed, fluid could be pressed from the stomach into the œso-

phagus by the inferior ribs being drawn down upon the epigastric region: they perceived no motion of the stomach itself, except the circular contractions in the neighbourhood of the pylorus, which, they say, occur independently of the act of vomiting.(?) Rudolphi, on the contrary, saw motion of the stomach during vomiting after the abdominal muscles had been divided.* Magendie's experiment with the pig's bladder does not prove much; and Rudolphi justly remarks that the tartar emetic injected into the veins in this experiment must have excited anti-peristaltic motions of the œsophagus, by which the contents of the stomach might be, as it were, pumped up, and the quantity of the fluid expelled in that instance was very small. The experiment, indeed, loses all its apparent importance when we consider that the condition which ordinarily prevents the escape of the contents of the stomach into the œsophagus,—namely, the contraction of the lower extremity of the œsophagus,—would not exist when the œsophagus was cut through, so that from the slightest cause any fluid would escape through it. But, independently of these circumstances, we may, like Rudolphi, demand with just indignation how the fact that a bladder having its contents forced from it into the œsophagus can prove that the stomach is passive in the act of vomiting? An important circumstance, which has hitherto been too much disregarded, is the existence of a kind of imperceptible contraction of the whole stomach, by which its entire volume is diminished without individual parts being seen to contract. I have often observed such a contraction of the stomach when vomiting was not taking place. The contraction of the stomach during vomiting appears to me to be an indubitable fact, for it can be felt by the person about to vomit, although it has not so great a share in the production of vomiting as has been ascribed to it.

Action of emetics.—The propagation of the local irritation of the stomach by sympathy to other muscles,—particularly the abdominal muscles and diaphragm,—is no longer a mere hypothesis; I have repeatedly found that by lacerating with a needle the nervus splanchnicus of the left side, at the inner border of the supra-renal capsule in the rabbit, I could produce contraction of the abdominal muscles. (In the dog the experiment did not succeed.) Now, since the nervus splanchnicus is the medium of communication between the sympathetic nerve and the cœliac ganglion, while the cœliac ganglion, again, is connected with the spinal nerves, and through them with the spinal cord; it follows, that irritation of the splanchnic nerve may be communicated either immediately, or through the medium of the spinal cord, to the nerves of the abdominal muscles. This observation, in my opinion, renders M. Magendie's

* In Lund's work (Vivisectionen, &c.) will be found the experiments on this subject by Portal, Bourdon, Beclard, and Merat, whose conclusions were opposed to Magendie's opinion; and others, by Rostan, Piedagnel, and Goudret, which were favourable to his view. But none of them are very decisive.

theory of the action of emetic medicines very improbable. He supposes that emetics introduced into the stomach are first taken up into the circulation, and thence affect the different organs concerned in the act of vomiting, in the same way as tartar emetic injected into the veins in other parts. If the splanchnic nerve has the power of exciting contractions of the abdominal muscles, that alone is almost sufficient to prove that the vomiting produced by substances taken into the stomach owes its production to the local irritation being propagated through the nerves, and when it is produced by mechanical irritation of the stomach or intestines, by inflammation of the stomach or intestines, or by mechanical irritation of the pharynx, it can be explained in no other manner.*

It being very probable, then, that emetics introduced into the stomach excite the movements of vomiting through the medium of nervous communication, the question arises whether the irritation in such cases is communicated to the brain by the vagus nerve especially, or to the brain and spinal cord by the splanchnic and sympathetic nerves, the auxiliary motions in the act of vomiting being in either case excited by the influence transmitted to the diaphragm and abdominal muscles from the brain and spinal cord through the medium of the spinal nerves. The experiment already mentioned, which shows that the splanchnic nerve has the power of exciting contractions of the abdominal muscles, is a proof that that nerve has a share in the propagation of the irritation. The fact that vomiting is produced by irritation of the pharynx, which is principally supplied by branches of the vagus, proves, on the other hand, that the vagus is implicated in it. It is therefore certainly probable that both vagus and splanchnic nerve act simultaneously in transmitting the irritation when emetic agents act on the stomach and intestine.

The vomiting which is excited by division or ligature of the nervus vagus† is to be explained in the same way. The irritation arising from the ligature of the nerve, and even from the contusion which attends its division, is communicated to the brain; and the inflammation of the ends of the nerve, which necessarily ensues, produces the same impression on the brain, through the medium of the portion of nerve still connected with it, as is produced by irritation of the extremities of the nerves in inflammation of the stomach itself; the same result—vomiting—follows in both cases. The division of other nerves, likewise,—of the optic nerve, for instance, in extirpation of the eye,—sometimes excites vomiting. The observation, that "quelque soit la dose que vous administriez les vomitifs et les purgatifs dans les chiens, à qui vous avez fait la section des nerfs vagues, leur impression devient nulle," is ad-

* See Magendie's Mémoire concernant l'influence de l'émetique, etc. Nouv. Bull. de la Soc. Philom. t. iii. p. 360.

† Mayer, in Tiedemann's Zeitschrift, ii. 62.

duced by Brachet* as an argument for the nervus vagus having a share in transmitting to the brain the irritation of the stomach, which excites vomiting. The observation itself, however, is opposed to the fact that vomiting ensues spontaneously in dogs after the division of the vagus.

When vomiting arises from an affection of the brain itself, the irritation is communicated in part directly to the stomach, and in part to the spinal nerves and to the diaphragm and abdominal muscles, in consequence of the spinal marrow being likewise affected. The usual opinion is, that the irritation being excited in the vagus nerve by the cerebral affection, that nerve excites contractions of the stomach: but this it is difficult to believe, for, distinct as are the contractions of the œsophagus which may be excited by irritation of the nervus vagus mechanically or by galvanism, I have never succeeded in producing even a single distinct contraction of the stomach, although I have made repeated experiments with that view on rabbits, and carnivorous and granivorous birds, and have employed the strongest mechanical irritation, and even a very powerful galvanic pile, the vagus being in the last case insulated. Even the muscular gizzard of birds cannot be made to contract in the slightest degree. M. Magendie and Mr. Mayo have made similar observations. The motions of the stomach, like those of the intestines, appear to be wholly dependent on the sympathetic nerve. The peristaltic motions of both continue when they are removed from their connections in the body; Wepfer observed this of the stomach, and others have noticed it with regard to the intestines.

The mode of action of emetics introduced into the circulation still remains for consideration. There is no very evident explanation for it, or rather we do not possess sufficient data to enable us to determine the question in a decided manner. It is in fact a matter of indifference whether an irritant is applied to the mere surface of an organ, or acts more directly on the parenchyma, through the medium of the blood which traverses it. Thus arsenic excites inflammation of the stomach, even when applied primarily to other parts of the body. Hence it appears probable that the tartar emetic introduced into the blood acts on the organs which participate in the act of vomiting through the medium of their blood-vessels. But it is still a matter of doubt whether its more important action is upon the organs from which the nervous energy for the movements of vomiting are derived, or upon the organs of motion themselves.

6. *Motions of the intestines.*—The *vermicular*, or *peristaltic movements* of the intestines, like those of the stomach, appear to be generally very feeble during life; it is only when an irritable state of the nervous system extends its effects to the intestinal canal, in dyspepsia, in spasmodic action of their muscular coats, particularly in intestinal irritation or diarrhœa, that the action of the intestines becomes more rapid: when

* Recherches sur les fonctions du Système Ganglionaire.

an animal is opened during life, the peristaltic motions are at first scarcely perceptible, but by exposure to the air they are soon increased in force, and become extremely energetic; the intestines rise and fall, and force onwards their contents, generally in the direction of the rectum. If a stimulus, whether mechanical or chemical, or the galvanic influence, be applied to any part of the intestines, contraction takes place, and the intestine by degrees becomes very narrow at that point, the greatest degree of contraction not taking place until after the action of the stimulus has ceased; the subsequent relaxation is likewise gradual. A strong galvanic shock applied to the splanchnic nerve insulated on a plate of glass, or to the cœliac ganglion, gives rise to a generally increased activity of the peristaltic movements, while division neither of the vagus nor of the sympathetic nerve puts a stop to them: they continue even after the intestine is removed from the body.

The *sphincter ani* is always in a contracted state except at the time of the evacuation of the fæces. It seems to have, in common with all muscles, a slight degree of the power of constant contraction, which does not become sensible until the antagonising muscles are divided. But the accumulation of the fæces in the rectum, and the irritation produced thereby, cause the contraction of the sphincter to become stronger, and it continues till it is overcome by the increasing pressure of the excrement. The sphincter may by an effort of the will be made to contract more strongly, but it cannot be made to relax. The contraction of the sphincter ani is in some rare cases overcome, and the fæces, when of soft consistence, expelled by the mere involuntary contraction of the rectum, without the aid of the abdominal muscles. Legallois and Beclard,* indeed, state that they have seen this occur after the abdominal muscles had been removed. Usually, however, the diminution of the capacity of the abdomen by the contraction of the diaphragm and abdominal muscles with the voluntary action of the levator ani, are necessary to effect the expulsion of the fæces. But all these voluntary muscles contract involuntarily and spasmodically, as in vomiting, when the irritation excited by the fæces has continued for a long time, and is become very great.

The *muscular action of the rectum* may be paralysed in consequence of injuries or disease of the spinal marrow (and brain), and this may give rise to incontinence or permanent retention of the fæces, according as the paralysis affects more particularly the sphincter ani or the rectum and abdominal muscles. Division of the phrenic nerves, and the consequent paralysis of the diaphragm, are said by Krimer not to prevent the expulsion of the fæces, although such is the effect in dogs, of dividing of the abdominal muscles, or the spinal cord between the fifth and sixth vertebræ.

* Bull. de la Fac. et de la Soc. de Méd. 1813. N. 10.

CHAPTER IV.

OF THE SECRETIONS POURED INTO THE DIGESTIVE CANAL.

1. *Saliva.*—There seems to be a secretion of saliva in almost all animals, with the exception of the cetacea and fishes. Whether the secretion of the poison glands with which some serpents* (and arachnida also) are provided, contributes to the solution of the food, is not known. The analogy which has been supposed to exist between such secretions and the saliva of rabid animals, is without foundation; for the poisonous property of the saliva in rabies is not an essential quality of it, and it appears from the experiments of Hertwig, at the veterinary school of Berlin, that other secretions of rabid animals, at all events their blood, are capable of producing the disease by inoculation. This does away likewise with the inference deduced from a circumstance which has been asserted to occur, namely, that the saliva has, under the influence of passion, become poisonous. The material changes in the body consequent on violent affections of the mind are general, implicating several secretions simultaneously; they have been particularly observed in the milk. It has not been proved that the bites of enraged animals differ from common lacerated wounds.

The *quantity of the salivary secretion* has been made the subject of observation by Dr. C. G. Mitscherlich in a man who had fistula of the stenonian duct. He found that when the muscles concerned in mastication, and the tongue, are completely at rest, and the nerves are subject to no unusual stimulus, the secretion ceases, but that it is excited by the opposite circumstances. The quantity of the saliva secreted by one parotid in a healthy man during twenty-four hours was from sixty-five to ninety-five grammes (about two to three ounces troy); and the saliva collected from the mouth during the same period, and derived from the five other salivary glands, amounted to six times more than that from the one parotid.† In the same space of time Schultz collected from the stenonian duct of a horse fifty-five ounces seven drams of saliva, of which twelve ounces were secreted during the first feeding-time, which occupied two hours; ten ounces nine drams during the three hours which elapsed between the first and second feed.‡

The *chemical composition of the saliva* has been examined in an admirable manner by Berzelius,§ by Gmelin,|| and by Mitscherlich.¶

* For an account of the effects of the bite of poisonous serpents, consult Fontana über das Viperngift; Berlin, 1787, p. 15; Traité sur le venin de la Vipère; and Rengger, in Meckel's Archiv. 1829.

† Mitscherlich, über den Speichel des Menschen. Rust's Mag. 1832.

‡ Schultz, de Aliment. Concoctione. Berol. 1834.

§ Chimie Animale.

|| Die Verdauung nach Versuchen. Heid. 1826.—Récherches sur la Digestion trad par Jourdain. Paris, 1826.

¶ Loc. cit.

The saliva obtained from the mouth is a viscous fluid, consisting of a mixture of saliva and mucus. Berzelius, having collected it in a deep narrow vessel, found that it separated into an upper transparent and colourless fluid, and a lower portion, which was a mixture of the same fluid and a white opaque matter. By previously mixing the saliva with water, and agitating them together, Berzelius was enabled to separate more completely the mucus, which sank to the bottom of the vessel.

Saliva varies as to acid or alkaline reaction. Tiedemann and Gmelin found it to be generally slightly alkaline, sometimes neutral, never acid. Schultz states that it is acid in the adult when it has been retained long in the mouth, but that it is always alkaline in children. The saliva of dogs and sheep collected from the parotid duct was found by Gmelin to be alkaline. C. H. Schultz also states as the result of his observation, that the saliva of the human subject is generally alkaline, one dram requiring one drop of acetic acid to neutralise it. He found the saliva of the horse also alkaline; and he asserts that, after the saliva had been neutralised, it gradually recovered its alkaline property. Dr. Mitscherlich found the saliva which he collected from a fistula of the parotid duct to be alkaline during a meal, but acid at other times. The alkalescence of the saliva is stated by Schultz to be dependent on the presence of ammonia. Mitscherlich, on the contrary, asserts that fresh saliva evolves no ammonia when heated, and that its alkaline property is owing to its containing a fixed alkali.

The specific weight of the fresh saliva obtained by Mitscherlich was 1·0061—1·0088; that of the horse's saliva, examined by Schultz, was 1·0125.

Saliva contains globules in very small number; they have been observed by Leeuwenhoeck, Weber, Tiedemann, and myself; they are transparent, and, according to Weber, larger than the red particles of the blood.

Berzelius estimates the amount of solid matter which saliva holds in solution at about 1 per cent. The mass which remains when saliva is evaporated, is transparent; alcohol extracts from it a small quantity of osmazome, with some chloride of sodium and potassium, and lactate of an alkali. The matter which is not dissolved by the alcohol, is slightly alkaline, and contains soda. The residue, when this soda is removed, is found to consist of mucus, which constitutes $\frac{1}{3}$rd, and a peculiar substance called salivary matter [which has been rather differently described by Berzelius, Mitscherlich and Tiedemann and Gmelin.†] From the mucus which remains after the extraction of the salivary matter with cold water, Berzelius obtained a large quantity of phosphate of lime, from

* Vergleichende Anatomie.

† [See their works just cited, and the systematic treatises on chemistry.]

which probably the tartar of the teeth is formed, since it consists of phosphate of lime.

The following are the results of Tiedemann's and Gmelin's analysis. By evaporating the saliva of the human subject, they obtained from 1·14 to 1·19 per cent. of solid residue; this yielded 0·25 part of ash, of which 0·203 were soluble in water, and 0·047 were earthy phosphates. 100 parts of the residue of diluted saliva gave:

A substance soluble in alcohol, insoluble in water, (fat containing phosporus) . . . . Matters soluble both in alcohol and water, (osmazome, chloride of potassium, lactate of potash, and sulpho-cyanuret of potassium . .	31·25
Animal matter soluble in boiling alcohol, but precipitated during cooling, with sulphate of potash, and some chloride of potassium . .	1·25
Matters soluble in water only, (salivary matter, with abundant phosphate and some sulphate of an alkali and chloride of potassium) . .	20·00
Matters soluble neither in water nor in alcohol, (mucus, perhaps some albumen, with alkaline carbonate and phosphate) . . .	40·00
	92.50

The saline ingredients of the saliva are, according to Dr. Mitscherlich:

Chloride of potassium	0·18	per cent.
Potash (combined with lactic acid) . . .	0·094	
Soda	0·024	
Lactic acid		
Soda (probably combined with mucus) . .	0·164	
Phosphate of lime	0·017	
Silicic earth	0·015	

The proximate organic principles obtained from the saliva by Mitscherlich are similar to those which Berzelius enumerates.

The matter which Tiedemann and Gmelin have shown to be *sulpho-cyanogen* was first discovered to be *an ingredient in the saliva* by Treviranus:* he found that saliva becomes of a deep red colour when mixed with a neutral solution of a salt of the peroxide of iron. This was confirmed by Tiedemann and Gmelin; but I must remark that, in my experiments, whatever per-salt of iron I might add, the colour produced was only rust-red, not purple-red.† Kuehn doubts the presence of sulpho-cyanogen in the saliva, because he could not give rise to the production of sulphuric acid in it either by Gmelin's or by Ure's process. If a red colour is really produced by the action of saliva on salts of the peroxide of iron, it may, he says, be owing to the presence of acetic acid, for the acetates do produce that colour when mixed with muriate of peroxide of iron.‡ To this remark of Kuehn, Kastner objects, that

* Biologie, iv. 565.

† See page 125.

‡ Kuehn, in Schweigger's Journal, 59. 378. See also Schultz, loc. cit.

the colour produced by acetic acid is never perfectly blood-red; but the colour which saliva gives rise to, is likewise not blood-red. Dr. Ure* regards the existence of sulpho-cyanogen in the saliva as established beyond all question by his experiments. (?)

Of the animal matters of the human saliva,—namely, salivary matter, mucus, and osmazome,—the first was found by Tiedemann and Gmelin to be almost wholly wanting in the saliva of the sheep, the last in that of the dog.

The *tartar which collects on the human teeth* has been analysed by Berzelius, who states its composition to be as follows:

Salivary matter	1·0
Salivary mucus	12·5
Earthy phosphates	79·0
Animal matter dissolved by muriatic acid	7·5
	100·0

The *saliva of insects* has not been accurately examined; it appeared to Rengger† to be alkaline.

2. *The gastric juice.*—The description given of the gastric juice by the earlier writers who made it the subject of examination, were completely contradictory. Spallanzani, who sought to prove that the gastric secretion is a solvent of the articles of food out of the body as well as in the stomach, asserted that it is perfectly neutral; while Montègre‡ found it to be generally acid, although he denied its solvent power. Helm § detected no acidity in the gastric fluid obtained from a patient who had a fistulous opening communicating with the stomach: Viridet, Carminati, Brugnatelli, and Werner, on the contrary, observed its acid property. The discrepancy of these statements was, however, in some measure explained by the experiments of Carminati,|| who found that the gastric fluid obtained from carnivorous animals while fasting was never acid, but became distinctly so as soon as food was taken. He remarked that the gastric juice of herbivorous animals also is acid, but detected no remarkable acidity in that of man and animals of mixed food. Tiedemann and Gmelin have finally determined the question. They ascertained that the fluid in the stomach of horses and dogs, while the animals were fasting, was nearly neutral, or only very slightly acid; but that it acquired a marked degree of acidity as soon as mechanical irritants, such as stones or peppercorns, were introduced into the stomach. Leuret and Lassaigne have made the same observation. It

* Journal of Science, Literature, and Arts, N. S. vii. p. 60.

† Physiol. Untersuch. über die thierische Haushaltung der Insecten. Tüb. 1817.

‡ Sur la Digestion. Paris, 1804.

§ Zwei Krankengeschichten. Wien, 1803. 8.

|| Über die Natur des Magensaftes. Wien, 1785. 8.

was the secretion of the stomach only that was acid in these cases; no acidity could be detected in the œsophagus.

The gastric juice had hitherto been examined by no one in such large quantity, in such a pure state, and so frequently, as by Dr. Beaumont, who, during several years, carried on a long series of experiments, relative to digestion on the youth, in whom a large opening communicating with the stomach remained after a gun-shot wound. Dr. Beaumont confirms the statement, that the stomach when empty secretes no gastric juice, and that the fluid which moistens its surface in that state is not acid, but becomes so as soon as food is taken. Schultz, who wholly denies the existence of a gastric juice, and attributes the acid reaction of the chyme to decomposition of the food itself, could not but perceive an objection to his theory in the fact observed by Tiedemann and Gmelin, that the secretion of gastric juice can be excited in animals when the stomach contains no food, by the introduction of mechanical stimuli, such as stones; and he explains the acid property of the fluid in the stomach in these cases by supposing it to be the remains of acid chyme. The numerous experiments of Dr. Beaumont, however, render it impossible for the existence of a gastric fluid to be any longer doubted. Having ascertained that the stomach was empty, and that its coats evidenced the presence of no free acid, he irritated it mechanically by introducing through the wound a caoutchouc tube, or the bulb of a thermometer, and observed each time, however often the experiment was repeated, that a pretty copious acid secretion was poured out; he was frequently able to obtain by this method nearly an ounce of the gastric juice.

The degree of acidity, which is an interesting point, has been investigated by Schultz; and from the mean of his observations it appears, that one part of chyme requires, for its neutralisation, $\frac{1}{100}$ of carbonate of potash.

The source of the gastric fluid seems to be the very simple follicles of the mucous membrane of the stomach, at least in those animals which have no special glands for its secretion. The structure of the mucous membrane of the human stomach has been already described.* Tiedemann and Gmelin found that the property of coagulating milk was possessed, not only by the pyloric, but also by the cardiac portion of the stomach. Dr. Beaumont states expressly that the secretion appeared to him to be poured out in the stomach of his patient by minute lucid points, or very fine papillæ. In several animals there are distinct gastric glands; we may instance the great gastric gland of the beaver, which most probably secretes a fluid destined for the solution of barks of trees; there is a similar gland in the cardiac portion of the stomach

* See page 494.

of the myoxus; and with these we may also class the proventiculus of birds, between the mucous and muscular coats of which there is a complete stratum of follicular cæca-like glands opening by separate mouths.*

Chemical analysis. — Dr. Prout† was the first chemist who instituted an accurate analysis of the gastric secretion. He showed that the gastric secretion of the rabbit, hare, horse, calf, and dog, contains free muriatic acid; and both Prout and Children‡ detected the same acid in the fluid raised from the stomach by dyspeptic patients. Prevost and Le Royer§ confirmed Prout's observation as to the presence of muriatic acid in the gastric juice. Leuret and Lassaigne, it is true, denied it, but Prout refuted their objections.

Tiedemann and Gmelin afterwards detected three acids in the gastric juice. 1. *Muriatic acid*, in the gastric juice of the horse and dog. 2. *Acetic acid*, in the gastric juice of the same animals. Chevreul has likewise found lactic acid, which is nearly allied to acetic acid, in the fluid vomited by a person fasting; and Dr. Graves has found it in the matter vomited by a dyspeptic patient. 3. *Butyric acid* was twice detected by the German physiologists in the stomach of the horse.

Schultz distilled the chyme with water, and found that in many animals a part of the acid or the whole of it passed over with the distilled fluid. He states, as the results of his experiments, that the acid of the chyme is free acetic acid; and that the muriatic acid is not free, but combined with potash.

The third and fourth stomachs only of ruminating animals are acid, and the acidity is most marked in the fourth. The fluid which collects in the first and second stomachs during fasting is said by Prevost and Le Royer to contain a large quantity of alkaline carbonate; Tiedemann and Gmelin have confirmed this observation.

Dr. Beaumont describes the secretion of the human stomach, which he obtained by irritating the stomach of St. Martin, as follows:—It is a clear transparent fluid, without smell, slightly saltish, and very perceptibly acid. Its taste resembles that of thin mucilage slightly acidulated with muriatic acid. It is readily diffusible in water, wine, or spirits, and effervesces slightly with alkalies; it precipitates albumen; itself undergoes putrefaction with difficulty, and checks its progress in other animal substances. Mixed with saliva, it strikes a blue colour and becomes frothy. Dr. Beaumont submitted a certain quantity for analysis to Professor Dunglison, who found it to contain free muriatic acid, acetic acids, phosphates and muriates of potash, soda, magnesia, and lime, and an animal matter which was soluble in cold, but insoluble in

* Sir E. Home's Lectures on Comparative Anatomy, t. ii.; and J. Müller, de Penit. Gland. Struct.

† Philos. Transact. 1824, p. 1.

‡ Annals of Philosophy. July, 1824.

§ Froriep's Notiz. ix. p. 194.

hot water. He sent another portion of it to Dr. Silliman likewise, whose analysis, however, loses its value, on account of the fluid having been kept several months before it was examined. It was still acid, although a pellicle had formed on it; it contained muriatic acid, a trace of sulphuric acid, and Dr. Silliman suspected the presence of some phosphoric acid.

The fluid of the crop of birds is, according to Tiedemann and Gmelin, usually acid. The secretion of the proventiculus contains a free acid, even at the time that digestion is not going on. The gastric secretion of birds coagulates milk. The acidity is owing to the presence of muriatic, and probably of acetic acid likewise. It has been suggested by Treviranus,* that the gastric secretion of birds probably contains fluoric acid, since Brugnatelli † has observed that rock crystal and agate enclosed in tubes, and introduced into the stomach of hens and turkeys, were, at the end of ten days, distinctly acted on, and had lost ten or twelve grains of their weight; and Treviranus himself witnessed a similar action on a porcelain capsule, in which some chyme from the stomach of hens had been digested. Tiedemann and Gmelin,‡ with a view to determine the question, digested some of the gastric secretion of ducks in a platina crucible which was covered with a glass plate, on which some device had been drawn through wax; but, at the expiration of twenty-four hours, no trace of any erosion of the glass was perceptible. They do not, however, hence infer that the gastric juice of birds does not contain fluoric acid; for fluor-calcium at least is met with in several animal tissues, as in the bones and in the urine.

The gastric secretion of reptiles is generally acid; in the stomach of fishes also, particularly when it contains food, there is a free acid. Other reasons render it probable that, in both these classes, the gastric secretion contains muriatic and acetic acids.

Leuret and Lassaigne § believe that the free acid of the stomach in all the four vertebrate classes is lactic acid. Eberle,|| however, has discovered that this acid is not the solvent principle of the gastric juice; but that the mucus of the stomach, (like all mucus, he says,) has the property, when acidulated, of inducing decomposition and subsequent solution of the food. And hence we find that with acidulated mucus of the stomach, artificial digestion of the food can be accomplished even out of the body.¶ Eberle was incorrect in stating that other mucus than that of the gastric mucous membrane is, when acidulated, adequate to

* Biologie, iv. p. 362. † Crell's Annalen, 1787, i. p. 230.

‡ Loc. cit. part ii.

§ Recherches Physiol. pour servir à l'Hist. de la Digestion. Paris, 1825.

|| Physiologie der Verdauung. Würzburg, 1834.

¶ See J. Müller and Schwann, über die künstliche Verdauung des geronnenen Eiweisses. Müller's Archiv. 1836, p. 66.

the solution of the food; and hence we may conclude that the solvent principle cannot be the mucus itself, but must be a peculiar substance contained in the mucus of the stomach. It is the same substance which causes the coagulation of the milk in the stomach. Most of what we know of the digestive principle, "pepsin," we owe to Schwann.* No method is at present known by which it may be obtained in a perfectly pure state. A further account of it will be given in the chapter on the digestive process.

3. *The bile.*—The bile is a secretion so generally met with in the animal kingdom, and so important in reference to the digestive process, that it would be in the highest degree interesting to know whether even in the lowest animals it is ever wholly wanting. We might regard, and some indeed have regarded, as the first form of the liver among the vermes, the sac-like dilatations or cæcal appendages of the intestinal canal, which are seen in the medicinal leech in their simplest form,—that of lateral dilatations,—in the aphrodita as long and narrow cæca, but which in other worms are ramified cæca; while in the planariæ and distomata, lastly, they assume the form of a completely ramified intestinal tube which has no anal opening. The cæcal appendages of the stomach of the asterias family, which likewise has no anal aperture, might be regarded as analogous secreting organs; but the nature of their secretion cannot be ascertained, nor indeed is it known that they secrete at all.

The long cæcal convoluted tubes which open into the intestinal canal of insects, generally in pairs, at a variable distance from the mouth and anus, but always below the dilated part of the canal which is supposed to be the stomach, have been called biliary vessels. They do not, however, contain bile, but, according to Chevreul† and Audouin,‡ uric acid: besides, they secrete very actively during the developement of the pupa, when no food is digested. They are, therefore, evidently excreting organs,—vasa urinaria. They open into the canal below the part where the chyle is formed, and in larvæ often but a short distance from the anus. I am, on the other hand, inclined with Meckel § to regard as biliary organs cæca which are met with in many insects opening into the intestinal canal higher up, either into the membranous stomach which succeeds the gizzard in the carnivorous coleoptera, or into the part of the canal just below the gizzard, as in many orthoptera, &c. In the arachnida,—for example, the scorpion,—there are true biliary vessels opening into the upper part of the intestine, and other Malpighian or excreting tubes at the lower part.||

* Über das Wesen des Verdauungs-prozesses. Müller's Archiv. 1836, p. 90.

† Strauss-Duerckheim's Considerations Générales sur l'Anatomie des Animaux Artic. Paris, 1828. 4. 251. ‡ L'Institut, 135. § Meckel's Archiv. 1826.

|| See J. Müller de Gland. Penit. Struct. Tab. viii. fig. 8.

Is the bile secreted from arterial or venous blood?—The liver of vertebrate animals receives two kinds of blood—arterial and venous; the sources of the venous blood carried to the liver by the vena portæ have been already described.* The distribution of the minute branches of the blood-vessels in the liver has been described at page 450; and the arguments are there stated, which render improbable Kiernan's opinion, that the branches of the hepatic artery do not contribute to the formation of one and the same general capillary network with the portal and hepatic veins, but are distributed solely to the coats of the ducts, gall-bladder, and the other blood-vessels; the blood carried by the artery after nourishing these parts being, according to his view, poured into branches of the portal vein. Mr. Kiernan believes the bile to be secreted from venous blood, while the arterial blood, according to him, serves for the nourishment of the tissues of which the liver is constituted, and for the secretion of the mucus in the gall-bladder, and in the ducts by the follicles which he has discovered in them.

But the possibility of bile being secreted from arterial blood is demonstrated by the cases in which the vena portæ enters the vena cava directly instead of being distributed through the liver. Mr. Abernethy† observed this anomalous structure in a male child ten months old; and Mr. Lawrence‡ has detailed a case in which the same malformation existed in a child several years of age. In Mr. Abernethy's case, however, the umbilical vein was still pervious, and branched out in the substance of the liver; it is possible therefore, as Mr. Kiernan remarks, that the arterial blood, after having nourished the liver, was poured into the branches of the umbilical vein, just as it is in the normal condition, according to his opinion, poured into branches of the portal vein; and the secretion of bile therefore might still have been derived from venous blood.§

M. Simon,‖ and Mr. B. Phillipps,¶ have inferred, from experiments which they performed, that the bile is secreted from the blood of the portal vein. But Mr. Phillipps found that after the vena portæ had been tied the secretion of bile still continued, though in diminished quantity; and he concludes, therefore, that it is formed both from arterial and venous blood. He perceived no change in the biliary secretion when the hepatic artery was tied.

With respect to the *quantity of the bile*, we have some observations by Schultz. In oxen which had not recently taken food, he found from twelve to sixteen ounces of bile in the gall-bladder; after digestion, it contained from two to four ounces. In a large dog, the gall-bladder con-

* Page 169. † Philos. Transact. 1793.

‡ Medico-chirurgical Transact. v. p. 174.

§ Kiernan, Philos. Transact. 1833, part ii.

‖ Nouv. Bull. des Sc. par la Soc. Philomat. 1825.

¶ London Medical Gazette, 1833. April 13.

tained, after a fast, five drams; in a middle-sized dog, just after digestion had been performed, it contained only two drams seventeen grains.

Properties of the bile.—The bile is a fluid of a green colour, bitter taste, and nauseous smell. The bile which flows from the liver is of a lighter colour: that obtained from the gall-bladder is less fluid and greener, on account of the more fluid part having been absorbed; and it is more viscid, owing to its containing mucus. It contains whitish or grey particles, which in the frog I found irregular in form and size; in the mean, five times smaller than the red particles of the animal's blood, others still more minute. The matter which gives to the bile its green colour is in solution. Bile is stated by Schultz to be, when fresh, always alkaline; when of thick consistence, one ounce required one dram of acetic acid for its neutralisation; when the bile was more fluid, the same quantity was neutralised by $\frac{1}{3}$ or $\frac{1}{2}$ dram of the acid. Schultz found the specific weight of the bile of the ox to be from 1·026 to 1·030. It does not coagulate at the boiling temperature, and does not dissolve oils. Werner asserts that bile added to the blood out of the body prevents its coagulation, and causes the red colouring matter to become dissolved in the serum; the latter statement, however, is incorrect.

The results of Berzelius's analysis of the *bile of the ox*, in 1807,* are as follows:

Alcohol dissolves, of bile evaporated to the consistence of an extract, all but a yellowish grey substance, which resembles in every respect the mucus of the gall-bladder. The alcoholic solution being evaporated to dryness, the addition of dilute sulphuric acid to a solution of the residue in a small quantity of water, throws down the "biliary matter" of Berzelius in combination with the acid, while the supernatant fluid retains in solution osmazome, chloride of sodium, and lactate of soda.

The compound of the biliary matter with the sulphuric acid has the characters of a resin. When the acid is separated by means of barytes, the biliary matter still contains a fatty matter; when freed from this fat by means of ether, it is soluble in water, alcohol, and the alkalies; the solution in water has the colour and taste of bile. The proportion of the different substances in the bile of the ox is, according to Berzelius:

Water	90·44
Biliary matter with fat	8·00
Mucus of the gall-bladder	0·30
Osmazome, chloride of sodium, and lactate of soda	0·74
Soda	0·41
Phosphate of soda, phosphate of lime, and traces of a substance insoluble in alcohol	0·11
	100·00

* See his Chimie. Animale.

Dr. Prout's analysis agrees in the essential points with that of Berzelius. M. Thenard in 1806, following another method of analysis, obtained from the bile of the ox two new substances, a green and bitter resin, and a yellow tenacious substance soluble in water and alcohol, which he calls "picromel" on account of its having a sweet and bitter taste.* The resin is soluble, Thenard says, in the picromel, and the solution is similar to bile. In one thousand parts of the bile of the ox, Thenard found:

Water	876·6
Biliary resin	30·0
Picromel	75·4
Yellow colouring matter	5·0
Soda	5·0
Phosphate of soda	2·5
Chloride of sodium	4·0
Sulphate of soda	1·0
Sulphate of lime	1·5
A trace of oxide of iron	
	1000·0

Berzelius has pointed out the probability that in place of these two constituents, biliary resin and picromel, there is in the bile really but one substance, his "biliary matter," which has the property of forming a resinous compound with mineral acids; and nitric acid was employed in Thenard's process of analysis. Gmelin, on the other hand, regards the "biliary matter" of Berzelius as a compound of several other substances, and supports the opinion of Thenard, that the bile contains picromel with a resin or some substance readily convertible into a resin.

The constituents of the bile of the ox are, according to Gmelin:

1. A musk-like odorous substance, which passes over with the water in distillation.

2. Cholesterine; the component of the gall-stones, shown to be an ingredient of fresh bile by Chevreul, and obtained from it by means of ether. It is found in other parts of the body,—according to Boudet, in the blood; but it is generally a morbid product; thus it is found in the fluid of local dropsies, such as hydrocele, and in medullary fungus.

3. Elaic acid.

4. Stearic acid.

5. Cholic acid, a new substance, which crystallises in fine acicular crystals of a sharp sweet taste, and soluble in alcohol. It contains nitrogen.

6. Biliary resin, which, according to Gmelin, contains no nitrogen.

7. Taurin, a new substance, which crystallises in large colourless,

* Mém. de la Soc. d'Arcueil, i. 23.

transparent, irregular six-sided prisms, with four or six-sided summits; is soluble in water, and contains a small quantity of nitrogen.

8. Picromel. Thenard's picromel is a thick fluid, like turpentine. Gmelin's picromel is opaque, consists of crystalline granules, and contains a large proportion of nitrogen. Gmelin believes that the substance which Thenard called picromel was a compound of that substance with resin.

9. Colouring matter of the bile; a substance containing nitrogen, which is recognised even when it is present in other fluids, such as the blood and urine in jaundice, by the addition of an equal quantity of nitric acid, striking a greenish, then a dark green, a dirty red, and, lastly, a brown colour.

10. Osmazome. 11. A substance which, when heated, gave out a urinous odour. 12. A substance like vegetable gluten. 13. Albumen. 14. Mucus of the gall-bladder. 15. Casein. 16. Salivary matter. 17. Bicarbonate of soda. 18. Carbonate of ammonia. 19. Acetate of soda. 20—26. Salts of elaic, stearic, cholic, sulphuric, and phosphoric acids, with potash and soda, chloride of sodium and phosphate of lime.

In *human bile* Gmelin found cholesterine, biliary resin, picromel, and elaic acid. Chevreul, Chevalier, and Lassaigne have also detected picromel in human bile; and Orfila, Laugier, and Caventou obtained it from human gall-stones. Besides the substances just mentioned, Frommherz and Gugert* have found in human bile colouring matter, salivary matter, casein, osmazome, salts of elaic, cholic, stearic, carbonic, phosphoric and sulphuric acids, with soda and a little potash, and phosphate, sulphate, and carbonate of lime.

Berzelius suggests that the bile in the natural state is probably a more simple fluid than would appear from the analytic results obtained by chemists, and that it is very likely that it contains the albuminous matters of the blood, in an altered state certainly, but combined with the same salts as in the blood itself; but that the product of the albuminous substances has so great a tendency to undergo changes in its composition, that the action of different re-agents upon it converts it into different compounds, which vary according to the processes employed to extract them, exactly as oils and fats are converted into sugar and fatty acids by the action of the oxides of lead and zinc.

Schultz considers the coagulum produced in bile by the addition of alcohol to be, not albumen, but a substance similar to salivary matter; and for this reason, that the bile does not coagulate under the influence of heat. The alcoholic solution of bile evaporated to dryness had still an alkaline reaction: but Schultz differs from most chemists in believing this alkalinity to be owing to the presence, neither of carbonates of the fixed alkalies, nor of ammonia, for the fluid obtained by distillation has,

* Schweigger's Journal, 50. 68.

he says, no alkalescence; but of an organic alkali similar to the vegetable alkaloids, which he supposes to exist in the bile in combination with elaic acid. The coagulum produced by acids he regards, not as albumen, but as precipitate of the alkaloid with the acid. But the substance which he obtained by the action of acetic acid was evidently the mucus of the gall-bladder, which is, according to Berzelius, precipitated from the bile by acetic acid; and Schultz himself remarks that the bile still retained in solution a bitter, or sweetish bitter, substance.*

Bile of serpents and fishes.—The bile of serpents was found by Berzelius to contain a peculiar substance, which is precipitated neither by acids nor by alkalies, and which differs from the "biliary matter" of warm-blooded animals in not being decomposed into picromel and biliary resin by acetate of lead. This biliary matter is combined with a colouring matter like that of the bile of other animals, which is entirely soluble in water while in combination with the biliary substance, the solution being perfectly similar to the bile itself, although, when separated from it, it is but slightly soluble. The bile of serpents contains in addition a small quantity of a crystallisable matter, which is precipitated by solution of carbonate of potash, and is analogous to the substance which Gmelin found in the bile of several species of cyprinus, (leuciscus, alburnus, and barbus,) and which in them holds the place of the biliary resin and picromel. Gmelin observed that this biliary matter of the fishes of the genus cyprinus, when added to bile, causes it to coagulate to a greenish-white granular mass.

The *bile of crustacea and mollusca* has not been examined.

Discharge of the bile.—The gall-bladder of vertebrate animals is developed as a diverticulum or protrusion from the efferent duct.† In man and many mammalia the flow of the bile into the intestine can be arrested either by the intestinal opening of the ductus choledochus being closed, or by prolonged contraction of the duct itself; and the bile, poured by the hepatic duct into the duct. chol. com. is thus made to regurgitate into the cystic duct and gall-bladder. It is more particularly during fasting that this takes place. In many animals, however, the gall-bladder receives bile by other hepatic ducts, which enter at its neck or at its fundus, and are called "ductus hepatico-cystici:" they do not exist in the human subject; but in birds they are the only means by which bile can reach the gall-bladder, for the hepatic duct opens into the duodenum distinctly from the cystic duct. In reptiles the bile is carried into the gall-bladder by branches of the hepatic duct. In

* [The account of the chemical composition of the bile has been abridged by the translator. For the chemical details of the different analyses he refers to the work of Berzelius on organic chemistry.]

† See J. Müller, de Gland. Penit. Struct.

fishes all the hepatic ducts coming from the different lobes enter the gall-bladder or its duct. In the ox, which is said by Rudolphi* to be the only one of the domestic animals in which the hepatico-cystic ducts exist, they are from eight to ten in number.

Many animals—mammalia, birds, and fishes—have no gall-bladder.† There seems to be no general law for its presence or absence, although the species in which it is wanting are for the most part herbivorous, and are animals in which digestion is constantly going on; yet very many vegetable feeders are provided with a gall-bladder. When the gall-bladder is wanting, the duct is frequently very much dilated; such is the case, for example, in the horse.

4. *The pancreatic secretion.*—We may almost regard the pancreas as an organ belonging exclusively to the vertebrate classes of animals; the two light-red lobulated glands attached to the biliary ducts in the loligo sagitata, pointed out by Dr. Grant‡ to be analogous to a pancreas, are the only exception.§ The pancreas is not constant in the class of fishes; it is in some entirely wanting; in others its place is supplied by cæca, called appendices pyloricæ, which vary in number and arrangement, becoming more and more divided as they are traced through different genera, until in the sharks and rays they are replaced by a solid gland.‖

The secretion of the pyloric cæca of fishes is adhesive, and, according to the observations of Swammerdam, and of Tiedemann and Gmelin, is not acid, or only very slightly so. The pancreas has been wholly, or in greater part, destroyed in dogs, without their digestion or general health suffering. In some few instances only greater voracity was observed after the operation.¶

The examination of the pancreatic secretion of the higher animals has been recently undertaken by Mayer, Magendie, and Tiedemann and Gmelin. Mayer** obtained it in some quantity from a vesicular reservoir in which it had collected in the cat; he found it alkaline and transparent. M. Magendie†† describes the pancreatic secretion of the dog as a yellowish fluid, without smell, of a saline taste, alkaline, and coagulable by heat, like that of birds. Tiedemann and Gmelin collected the secretion of the pancreas in a large dog by means of a tube introduced through an incision into the duct. A drop issued every six or seven seconds, nearly ten grammes, (about two and a half drams,) in four

* Physiologie, ii. pt. ii. p. 153.

† See Cuvier's Leçons d'Anatomie Comparée.

‡ Froriep's Notiz. xi. 182.

§ [The glandular laminated sac which opens into the intestine near the pylorus in the cephalopods, and which is of a globular form in the nautilus, elongated and spirally twisted in the loligo and octopus, is considered by Mr. Owen to be, like the pyloric cæca of fishes, the true analogue of the pancreas. See Cyclopedia of Anatomy, Art. Cephalopoda.]

‖ See page 447.

¶ Autenrieth, Physiol. ii. 69.

** Meckel's Archiv. iii. p. 170.

†† Physiologie, t. ii. p. 367. Dr. Milligan's translation, fourth edition, p. 461.

hours. It was clear, though somewhat opaline, ropy like white of egg in water, and had a slightly saline taste. They obtained some in the same manner from the sheep and goat. In all three cases the fluid which first flowed was acid; the latter portions only were slightly alkaline in the dog and horse. A. Schultz found the pancreatic secretion of the dog, cat, and horse, acid; once only, in the dog, it was neutral. The comparative analysis of the secretion in the dog, sheep, and horse, afforded Gmelin the following results: the pancreatic secretion contains a large quantity of albumen; no sulphocyanic acid salts, which the saliva is said to contain, can be detected in it. The solid matter which it holds in solution amounts in the dog to 8·72 per cent.; in the sheep, to from four to five per cent. The different solid ingredients are:

1. Osmazome; 2. a matter which is reddened by chlorine, and which is found only in the dog and sheep; 3. a substance resembling casein, combined probably with salivary matter; 4. a large quantity of albumen, amounting to about half of the dry residuum; 5. a very small proportion of free acid, probably acetic acid.

The ash left after calcination of the dried evaporated secretion amounted in the dog to 8·28 per cent., in the sheep to 29·7 per cent.; it contained the following soluble salts: 1. carbonate of potash, which is probably in the state of acetate in the secretion, (found in the dog and sheep); 2. abundance of alkaline muriate; 3. a small quantity of alkaline phosphate, (in the dog and sheep); 4. a very small quantity of alkaline sulphate, of which the base was more soda than potash, (also in the dog and sheep). The insoluble salts contained in the ash were small quantities of carbonate and phosphate of lime. A comparison of the pancreatic juice with the saliva, founded on the data furnished by the above excellent analyses of the pancreatic secretion, gives the following results. The saliva contains mucus and salivary matter; the pancreatic juice, on the other hand, contains an abundance of albumen and casein, no mucus, and little or no real salivary matter: saliva is alkaline; the pancreatic secretion, while fresh, is acid. The saliva of the sheep contains a small quantity of sulphocyanate of an alkali (?); the pancreatic juice, none. The other salts are about the same in both.*

Leuret and Lassaigne obtained three ounces of secretion from the pancreas of a living horse in half an hour. It was clear, had a saline taste, an alkaline reaction, and contained only $\frac{9}{10}$ per cent. of solid constituents, which, after an examination apparently superficial, they concluded to be the same as in saliva. The statement of their analysis is as follows: Water, 99·0: animal matter soluble in alcohol, animal matter soluble in water, traces of albumen, mucus, free soda, chloride of sodium, chloride of potassium, and phosphate of lime, 00·9.

5. *Intestinal secretion; succus entericus.*—The secretion of the intes-

* Tiedemann and Gmelin, loc. cit.

tines has been examined in animals which had fasted for some time by Tiedemann and Gmelin. In dogs the inner surface of the mucous membrane was found covered with a thin layer of a very consistent, whitish, and somewhat yellowish matter; the intestines contained very little bile. If flint pebbles, or peppercorns, had been previously swallowed, there was a larger quantity of a thin ropy mucus, and more bile. The mucous mass became more consistent towards the lower part of the small intestines, acquired a yellowish or yellowish-brown colour, and contained greenish yellow or yellowish-brown flakes, which consisted of intestinal mucus, biliary mucus, with the resins, fatty matter, and colouring matter of the bile. The mucous fluid in the upper third or upper half of the small intestines of the dog and horse, contained,

1. Some free acid (lower down in the canal the secretion was for the most part neutral, and in the horse contained bicarbonate of soda).
2. Albumen, in considerable quantity, — probably derived from the pancreatic juice.
3. (In the horse) a matter similar to casein.
4. (In the same animal) a substance precipitated by muriate of tin,— probably salivin and osmazome.
5. (Also in the horse) a matter which is reddened when acted on by chlorine or oxymuriate of mercury.
6. A small quantity of biliary resin.
7. (In the upper part of the small intestine of the horse) a feebly acid substance which contains nitrogen.
8. The usual salts of the animal fluids.

The mucus of the cæcum in dogs was always acid. In the horse, on the contrary, it contained bicarbonate of soda.

Viridet* had previously observed that in the rabbit the cæcum evidences the same acid reaction as the stomach.

Schultz has instituted some further experiments relative to the acid secretion of the cæcum. He found that when the animals had fasted the fluid in the cæcum was more frequently alkaline or neutral, although at other times, and during digestion, it was acid; this difference he supposed to arise from the bile reaching the cæcum during fasting and neutralising the acid. It was, however, chiefly in herbivorous animals, which have a long cæcum, that he met with the acid reaction; in the carnivora, in which the cæcum is less developed, there was generally no acidity. Two ounces of chyme taken from the stomach of a rabbit which had been fed with potatoes and grass, and was opened two hours and a half after death, required for saturation three ounces and a half of ox's bile; to neutralise one ounce of the contents of the cæcum of the rabbit five drams of the bile were required. Eighteen ounces of chyme from the stomach of a horse required fifteen grains of carbonate of

* De Primâ Coctione.

potash, or two ounces and a half of bile of the ox to one ounce of the chyme; while for one ounce of the contents of the cæcum five ounces of the bile were necessary. The chyme from the stomach of a hog required for saturation from 1·04 to 1·11 per cent. of carbonate of potash; the contents of the cæcum, on the other hand, required only 0·78 per cent.

CHAPTER V.

OF THE CHANGES WHICH THE FOOD UNDERGOES IN THE ALIMENTARY CANAL.

Before the solution of the food can take place, it is necessary that the different substances which are used as aliment should lose their organic structure and cohesion; this is effected principally by mastication. The division of the food is performed either in the mouth,—or in the pharynx, where pharyngeal teeth exist, as in fishes,—or in the stomach itself, which then has either cartilaginous parietes, as in the granivorous and insectivorous birds, or teeth, as in some crustacea, insects, and mollusca. Mastication, and the subsequent stage of the digestive process, may, in fact, be compared with the usual chemical operations; it is not necessary to ascribe any share in them to organic influence. The chemist reduces to powder the substances which he wishes to dissolve, or from which he desires to extract a particular ingredient, and then digests them in the solvent menstruum; a similar digestion is performed in the crop of birds and in the stomach. After the soluble portion has been dissolved, the chemist separates it by filtration; and in the digestive process, after the trituration and solution, there is likewise a separation of the dissolved from the insoluble parts.

a. Change effected by the saliva.—The saliva prepares the food mechanically for deglutition; whether it contributes in any degree to the solution of the food, and what share its components have in the production of the chemical change in the stomach, are unknown. But, since fishes and cetacea are not provided with the salivary secretion, it would appear to play by no means an important part in the process. Spallanzani and Reaumur state, as the result of their experiments, that food enclosed in perforated tubes, and introduced into the stomach of animals, was more quickly digested when it had been previously impregnated with saliva than if it was merely moistened with water.* Tiedemann and Gmelin, too, believe that the carbonates, acetates, and muriates of potash and soda, which enter into the composition of the saliva, give it a solvent property, although a slight one. (?) Berzelius, on the other hand, observes, that saliva alone has no more action on alimentary substances, dissolves no greater part of them, than pure water;

* Spallanzani, Versuche über das Verdauungsgeschäft. Leipz. 1785.—Expériences sur la digestion, par Sennebier. Genève, 1783.

and I must confess that I have perceived scarcely any difference between the action of saliva and that of water on meat in experiments instituted for the purpose of comparison.

The so-called dynamic effects of the saliva I am wholly unacquainted with. Nor does the saliva appear to act by destroying the peculiar organic properties of the alimentary substances. The action of the poisonous secretion of serpents, and of the saliva of rabid animals, might induce a belief in the saliva having such properties; but that, as I have already remarked, the glands which secrete the poison in the poisonous serpents are distinct from the salivary glands, which are present in addition to the poison glands,—these latter being special instruments of offence. The infectious principle of rabies, too, is not a property of the saliva alone, but is possessed by all the fluids of the body of the rabid animal.*

The only fact favourable to the opinion that the saliva has a share in the chemical process of digestion in the stomach, is that observed by Leuchs,† and confirmed by Schwann,—namely, that saliva has the property of changing starch into sugar, which is interesting, inasmuch as starch is in the stomach converted into gum of starch, and gradually into sugar.

b. Change which the food undergoes in the stomach,—action of the gastric juice.—The fluids taken into the stomach are for the most part absorbed from it, and do not even pass the pylorus. The solids are, with the exception of the insoluble parts, reduced to a substance called chyme, which is in part quite fluid, in part consists of globules. The formation of chyme is described by most observers to go on solely at the surface of the food which is in contact with the coats of the stomach; but Dr. Beaumont observed in his numerous experiments that the gastric juice acts at the same time on each and every particle of food in the stomach, and not merely on the surface of the whole mass.

Observations relative to the changes which the food undergoes in digestion, and the time occupied by these changes, have been instituted by Gosse, who for that purpose excited artificial vomiting in his own person;‡ by Spallanzani, Stevens,§ Tiedemann and Gmelin, and Schultz, on animals; and, lastly, by Dr. Beaumont in far greater number than by any other physiologist.

Spallanzani introduced a tube filled with bread into the stomach of a cat; in five hours the bread was partly dissolved; for the solution of meat nine hours were required. Even cartilages and bone contained in tubes, and tendons enclosed in linen, were after a longer period softened or dissolved.

* Hertwig's Beiträge zur näheren Kentniss der Wuthkrankheit. Berl. 1829, p. 156. 160. † Kastner's Archiv. 1831. ‡ His experiments are detailed by Spallanzani. § De Aliment. Concoct. Edinb. 1777.

Tiedemann and Gmelin having given dogs boiled white of egg to eat, and killed the animals four hours afterwards, found the particles of that substance in part dissolved. Fibrin in the same space of time had become swollen with moisture, and was partly converted into albumen, which was in solution. They found that animal gelatin loses by digestion in the stomach its property of gelatinising spontaneously, and its peculiarity of being precipitated in shreds by chlorine. Cheese was dissolved without being converted into albumen. Boiled starch was in the course of a few hours converted into gum of starch and sugar. Vegetable gluten, which is insoluble in acetic and muriatic acids, was found unaltered after having been in the stomach five hours. Milk is coagulated; the whey is then removed by absorption, while the curds are redissolved. Raw beef, after having been four hours in the stomach, was found covered with a brown, pulpy, gelatinous mass. Cartilage and bone, after being digested for from two to four hours, appeared somewhat softened at the angles, edges, and surface. Bread was in two and a half hours almost completely dissolved. In the horse the food seemed to leave the stomach in a state less advanced towards solution.

Dr. Beaumont has had the rare opportunity of studying during several years the process of digestion in a man, named St. Martin, who came under his care in consequence of having received a gun-shot wound which left an opening two inches below the left mamma, in a line drawn from that part to the left spine of the ilium, which communicated with the stomach at its upper part, near the upper extremity of the great curvature, and three inches from the cardiac orifice. The borders of the opening into the stomach, which was considerable, had united in healing with the margins of the external wound, but the cavity of the stomach was at last cut off from the exterior by a fold of mucous membrane which projected from the upper and back part of the opening, and closed it like a valve, but could be pushed back by the finger. If, while St. Martin lay on his back, pressure was made with the hand in the situation of the liver, and the body turned at the same time upon the left side, bile flowed through the pylorus, and could be drawn off by an elastic gum tube introduced into the stomach. Sometimes, too, though rarely, bile was found mixed with the gastric juice when the above manœuvre had not been practised. Chyme was obtained from the stomach by applying the hand to the lower part of the epigastric region, and directing pressure upwards. When the stomach was full, mere pressure upon the valvular fold which closed the opening was sufficient to cause an escape of the contents. The stomach while empty could be explored to the depth of five or six inches by artificial distention. The food and drink could in this manner be seen to enter it.

Dr. Beaumont has kept a complete journal of the digestive process in this man. The following table shows the time required for the diges-

tion of different kinds of food, which were taken with bread or vegetables, or both.

Articles of diet.	Mode of cooking.	Meal.	Exercise. Moderate	Exercise. Increased	Rest.	Remarks.
			h. m.	h. m.	h. m.	
Tripe, soused	fried ..	breakfast	1 0			
Pigs' feet, do.	boiled ..	——	1 0			
Venison steak, fresh ..	broiled ..	——	1 35			
Codfish, dry ..	boiled ..	dinner	2 0			
Bread and milk	cold ..	——	2 0			
Turkey ..	roasted ..	——	2 30			
Goose, wild ..	——	——	2 30			
Pig, young ..	——	——	2 30			
Hash'd meat and vegetables	warm ..	breakfast	2 30			
Oysters ..	raw ..	dinner	2 45	..	..	oysters suspended in the stomach.
——	stewed ..	——	3 30	..	..	nothing but a little dry bread or cracker taken at these meals.
——	raw ..	breakfast	3 0	..	..	
——	——	dinner	3 0	..	..	
——	stewed ..	——	3 30	..	..	
Beef, fresh, fat and lean ..	roasted ..	dinner	3 30			
——	——	——	3 0			
——	——	breakfast	2 45			
——	broiled ..	——	3 0			
——	——	——	—	..	3 45	
——	——	——	—	3 30	..	exercise till fatigued.
——	boiled ..	——	4 0	..	..	morbid appearance of stomach.
——	——	dinner	—	3 30		
——	——	breakfast	3 38	..	..	large proportion of fat.
——	——	supper	—	..	4 0	ditto.
——	——	breakfast	—	..	4 30	ditto, and in recumbent position.
——	——	dinner	3 30			
——	——	——	—	..	4 0	
——	——	breakfast	—	..	4 15	
——	——	——	3 30			
——	——	——	—	..	4 15	
Beef, salted ..	——	dinner	5 30			
——	——	——	3 30			
Pork, recently salted ..	——	breakfast	5 15			
——	——	——	4 30			
——	——	——	5 15	..	..	became angry during the experiment.
——	——	——	6 0	..	..	unusually full meal.
——	——	——	4 30			
——	——	——	4 30			
——	——	——	4 30			
——	——	dinner	4 30			
——	——	breakfast	—	4 0		
——	——	dinner	—	3 30		

Articles of diet.	Mode of cooking.	Meal.	Exercise. Moderate	Exercise. Increased	Rest.	Remarks.
			h. m.	h. m.	h. m.	
Pork, fresh ..	roasted ..	dinner	6 30	..	..	unusually full meal.
——	broiled ..	——	3 15			
——	——	breakfast	4 30			
Mutton, fat & lean	roasted ..	dinner	3 15			
——	broiled ..	breakfast	..	3 0		
——	——	——	3 30			
——	——	——	4 30	..	..	morbid appearance of stomach.
——	——	dinner	4 0			
——	——	breakfast	4 30	..	..	full meal coarsely masticated.
Eggs ..	hard-boiled	——	3 30	..	..	bread, or bread and coffee.
——	soft-boiled	——	3 0			
——	hard-boiled	dinner	5 30	..	..	morbid appearance of stomach.
——	——	breakfast	3 30	..	..	ditto.
——	soft-boiled	dinner	3 0			
Sausages ..	broiled ..	breakfast	3 30	..	..	with soft-boiled eggs.
——	——	dinner	3 0			
——	fried ..	breakfast	4 0	..	..	muslin bag, containing the same kind of diet, suspended in the stomach during these experiments; morbid appearance of stomach also.
——	——	——	5 0	..	..	
——	broiled ..	——	3 30	..	..	
——	——	——	..	4 15	..	full meal, severe exercise.
Fowls (hens) ..	boiled ..	——	4 0	..	..	with bread and coffee.
——	——	dinner	4 0	..	..	with bread and water.
——	——	——	4 0			
Veal, fresh ..	broiled ..	breakfast	4 0	..	..	muslin bag suspended in stomach.
——	——	dinner	4 0			
——	——	breakfast	4 0			
——	——	dinner	4 45	..	..	morbid appearance of stomach.
——	——	breakfast	..	3 45		
——	——	dinner	4 30			
——	——	breakfast	5 30	..	..	ditto.
Soup made of meat and vegetables	.. ..	——	4 0			
Bread buttered, with coffee	.. ..	——	4 15	..	..	ditto.
Bread dry, with coffee ..	.. ..	——	3 45			
Bread dry, with dry mashed potatoes ..	.. ..	dinner	3 45			

We transcribe some of the experiments from Dr. Beaumont's journal as examples. They are not without interest.*

Second series, Exp. 33.—At one o'clock St. Martin dined on roast-beef, bread and potatoes. In half an hour examined contents of stomach, found what he had eaten reduced to a mass resembling thick porridge. At two o'clock nearly all chymified,—a few distinct particles of food still to be seen. At half-past four, chymification complete. At six, nothing in the stomach but a little gastric juice tinged with bile.

Exp. 42.—April 7th, 8 A.M. Breakfast of three hard-boiled eggs, pancakes, and coffee. At half-past eight o'clock, examined stomach, found a heterogeneous mixture of the several articles slightly digested. At a quarter past ten, no part of breakfast in the stomach.

Exp. 43.—At eleven o'clock, same day, St. Martin ate two roasted eggs and three ripe apples. In half an hour they were in an incipient state of digestion; and at a quarter past twelve no vestige of them remained.

Exp. 44.—At two o'clock P.M. same day, dined on roasted pig and vegetables. At three o'clock they were half chymified, and at half-past four nothing remained but a very little gastric juice.

Third series, Exp. 18.—On December 17, half-past eight A.M. two drams of fresh fried sausage in a fine muslin bag suspended in the stomach of St. Martin, who immediately afterwards breakfasted on the same kind of sausage, and a small piece of broiled mutton, wheaten bread, and a pint of coffee. At half-past eleven, stomach half empty; contents of bag about half diminished. At two o'clock P.M. stomach empty and clean; contents of bag all gone except fifteen grains, consisting of small pieces of cartilaginous and membranous fibres, and the spices of the sausage, which last weighed six grains.

[Exp. 26, second series, — in which Dr. Beaumont examined the state of the food at intervals during the process of digestion,—shows very clearly that animal substances are dissolved much more rapidly than vegetables.]

Dr. Beaumont has observed that *the temperature of the stomach* does not become elevated during digestion; it is constantly 100° Fahr. and it is only during muscular exertion that it rises some degrees, like the temperature of other parts of the body.

The gas contained in the stomach is during digestion generally very

* [The translator has omitted the first experiment, since Dr. Beaumont himself points out that the apparent results of it cannot be depended on. It is interesting, however, that] during the experiment the boy complained of distress and uneasiness at the stomach, and that on the following day the same symptoms continuing, with pain of head, costiveness, a depressed pulse, dry skin, and coated tongue, numerous white spots or pustules resembling coagulated lymph were seen spread over the inner surface of the stomach, and that Dr. Beaumont has observed a similar appearance of the stomach on other occasions attending symptoms of indigestion.

small in quantity. Magendie and Chevreul obtained some from the stomach of an executed criminal, and found it to consist of

Oxygen	11·00
Carbonic acid	14·00
Hydrogen	3·55
Nitrogen	71·45

The components of the chyme, according to the analysis of Tiedemann and Gmelin, are:

1. Albumen,—in the chyme of dogs which had been fed with boiled eggs, fibrin, meat, bread, and vegetable gluten; it was less in quantity when the dogs had eaten liquid white of egg, cheese, glue and bones.

2. A substance resembling casein, — in the chyme of dogs fed with liquid white of egg and fibrin.

3. A substance precipitated by muriate of tin (probably osmazome and salivary matter),—in chyme resulting from the digestion of vegetable gluten, cheese and milk, in dogs, and of starch and oats, in horses.

Dr. Marcet pointed out,—and his observation has been confirmed by Dr. Prout,—that the chyme in dogs contains much more albumen when the animal has been fed on animal substances than when it has been fed with bread.*

Digestion in ruminants.—The fluid expressed from the mass of food in the first and second stomach of ruminating animals, is stated as well by Tiedemann and Gmelin, as by Prevost and Le Royer,† to contain albumen in solution by an alkali, which in the state of carbonate is an ingredient of the secretion of these cavities. The proportion of albumen in the fluid varies; when the food consisted of oats, it was in such abundance that it coagulated at the temperature of 158° Fahr. A developement of gas consisting of sulphuretted hydrogen, carbonic acid, and carburetted hydrogen, of which the two former are dissolved in the fluid, while the last retains its gaseous form, takes place during digestion in the first and second stomachs.‡

The contents of the fourth stomach, which is even more acid than the third, were found by Tiedemann and Gmelin to be in the calf coagulated milk, in the ox a soft yellowish brown pulp.

The components of the chyme in the fourth stomach were:

1. Albumen,—in the ox and calf.

2. A substance reddened by the action of muriatic acid,—in the ox and sheep.

3. A substance precipitated by muriate of tin,—in the sheep.

Digestion in birds.—The fluid resulting from the digestion of the food

* Thomson's Annals of Philos. 1819.

† Biblioth. Universelle de Genève, t. xxvii. p. 229.

‡ Berzelius, Chemie Animale.

in the crop of birds, was found by Tiedemann and Gmelin to contain albumen in a state of solution, and in such large proportion that the fluid was sometimes coagulable by heat; the coagulating substance being animal albumen when the food of the bird had been meat, vegetable albumen when the food had consisted of corn and peas. The albuminous matters were still more abundant in the muscular gizzard.

Theory of digestion.

Many of the older theories of the digestive process,—for example, that which supposed it to consist in attrition by the stomach,—are now evidently of mere historical interest. In by far the greater number of animals, the stomach is unprovided with mechanical instruments for the aid of digestion;* and the experiments of Reaumur and Spallanzani have demonstrated that substances enclosed in perforated tubes, and consequently protected from mechanical influence, are not less easily digested. It is, in like manner, scarcely necessary to remark that the theory of digestion by putrefaction is equally groundless; no signs of putrefaction being presented by the digested food, although, if the same substances were left to spontaneous decomposition at the temperature of $99\frac{1}{2}°$ Fahr., they would very quickly evidence marks of the putrefactive process. Moreover, when substances in which putrefaction has already commenced are subjected to digestion in the stomach, the putrefactive change is, as Spallanzani has shown, immediately checked in them.

In the present state of our knowledge of the subject, we have in the first place to decide,—

1. Whether digestion consists essentially in the articles of food undergoing in the stomach some chemical change, such as fermentation or oxidation, by which they are deprived of their cohesion and reduced to a pulp, there being no gastric solvent fluid,—the so-named gastric juice being, according to this view, the product, not the cause, of digestion.

2. Or whether digestion is really a solution of the food by a solvent menstruum,—the gastric juice.

We recognise the first of these views in the fermentative theory of Boerhaave, and it has been recently brought forward anew by C. H. Schultz in his hypothesis of the reduction of the food by oxidation.

The theory of digestion by fermentation does not, however, preclude the existence of an active gastric fluid. The theory of fermentation supposes that the food is reduced by a chemical action of its components on each other, this action being excited by a portion remaining from the last digested food, or by a ferment secreted by the stomach

* See page 487, et sequent.

itself, the acids of the stomach being the product of the fermentation. This theory has never been confirmed by proofs, and can now, indeed, be refuted.

The fermentation, if it exists, must be different from all other known kinds of fermentation; for, as we shall presently show, none of the usual phenomena of that process are present when digestion is performed artificially.

Schultz does not, it is true, set out on the supposition of the existence of a fermentative process in digestion; but still his theory is in principle similar, inasmuch as he supposes that the food is not dissolved by a peculiar fluid, but undergoes decomposition, and loses its cohesion, in consequence of being oxidised,—that the acid of the chyme is not the cause of this change, but the product of it.

The existence of a special digestive fluid had been already denied by Montègre. Having found that, after vomiting and neutralising any fluid that remained in his stomach by means of magnesia, food was still digested, and an acid chyme produced, he concluded that the fluid which is called gastric juice is nothing more than saliva and gastric mucus changed by the process of chymification. But it is evident that here the chymification might with equal probability be ascribed to the secretion of fresh gastric juice.

The arguments adduced by Schultz in support of his theory are first,—that no special solvent gastric secretion exists; that the matter regarded by Tiedemann and Gmelin as such, was merely a remaining portion of chyme; that no acids are formed in the stomach except during digestion, and that their production cannot be excited by mechanical irritation of the coats of the stomach. This statement is, however, at least contradicted by the concordant results of direct observations, not only those of Spallanzani, and Tiedemann and Gmelin, but also the much more conclusive experiments of Dr. Beaumont. Secondly,—Schultz adduces the analogy of vegetables, in which the nutritive matters undergo a change of this sort, and the nutritive material of the germinating seeds is converted by a kind of oxidation into acids and sugar, and rendered soluble. These arguments are very ingenious; but the question is, whether in animals there really is not a peculiar fluid secreted by the stomach which will dissolve the articles of food even out of the body? and even if we disregard the imperfect experiments of earlier physiologists, we shall find it satisfactorily proved by the numerous observations of Beaumont, Eberle, and others, that there is such a fluid. Lastly,—Schultz adduces the fact of the coagulation of the milk in the stomach as an example of the conversion of a substance which is not acid into an acid chyme. Milk is coagulated, he says, by an infusion of the stomach of a calf which has been dried and deprived of its acidity by neutralisation with carbonate of potash, and even by an

infusion of the fresh stomach of a dog which had been made to fast forty hours, so that the stomach was disticntly alkaline; and lastly, milk will coagulate, he remarks, in the stomach of sucking whelps after the stomach had been free from food during twelve or sixteen hours, and is neutral or alkaline; the only difference being that the coagulation takes place more slowly than when the stomach contains acids. It is quite true, as Berzelius had already pointed out, that the acid alone is not the cause of the coagulation of the milk; for the coagulation is now known to be due to a peculiar organic principle of the gastric secretion.

In the state of the inquiry, nearly up to the present time, the questions to be decided were: 1. Whether a gastric juice exists; 2. whether this gastric juice, whatever its nature, has the property of dissolving the substances used as food, not only in the stomach, but also out of the body; 3. whether, the last question being answered in the affirmative, the solution be effected by the agency of the acid ingredients of the gastric juice, or by some other principles which it can be demonstrated to contain; and 4. whether the solution is attended likewise with a change in the chemical composition of the alimentary substances.

1. *Is there a special gastric juice?* — This question has been already decided in the affirmative in the preceding chapter, in which were related the numerous experiments of Tiedemann and Gmelin, and the still more conclusive observations of Dr. Beaumont, who excited in St. Martin by mechanical irritation the secretion of gastric juice when the stomach contained no food, and collected it in considerable quantity by means of a tube introduced through the accidental opening into his stomach.

2. *Has the gastric juice the property of dissolving the food submitted to its action, whether in the stomach or out of the body?*—The answer to this question depends wholly on our being able, or not, to dissolve food artificially by means of gastric juice mixed with it out of the body. Attention was first directed to artificial digestion by the experiments of Spallanzani. That physiologist obtained some of the secretion of the stomach of birds by causing them to swallow small pieces of sponge which he withdrew after some little time by means of threads attached to them; the fluid thus obtained he mixed with food previously masticated, and put the mixture into small glass vessels in which he kept up the proper warmth by placing them in his axillæ. The contents were, after the lapse of fifteen hours or two days, found to be apparently converted into chyme. The statements of Spallanzani seemed, however, to be refuted by the observations of Montègre, which were submitted to the French Academy in 1812. The gastric fluid which Montègre employed in his experiments was the secretion of his stomach during fasting, which he had the power of vomiting at will; it was in most cases dis-

tinctly acid. Dr. Stevens obtained from artificial digestion a result similar to that announced by Spallanzani.

More recently, Tiedemann and Gmelin have instituted similar experiments with gastric fluid obtained from two dogs.

In the first experiment, three grammes (about forty-six grains) of boiled beef were submitted to the action of ten grammes (about two and a half drams) of the gastric fluid; in a second vessel, a cubic mass of bread freed from crust with the same quantity of the fluid; and in a third and fourth, similar portions of meat and bread were placed, each closely enveloped in a piece of the mucus coat of the stomach; lastly, similar portions of meat and bread were placed in a fifth and a sixth vessel with water. All the vessels were exposed during a period of eight hours to a temperature of from 86° to 104° Fahr. At the end of that time, the meat in the gastric juice was reduced at its surface to a reddish-white, very soft pulp, which could be easily scraped off; the meat enveloped in the mucous membrane had no such pulpy layer covering it, and was but little softer than that which had been macerated in pure water; the latter was quite hard, and nothing perceptible could be scraped from its surface. The bread in the gastric juice was converted into a soft whitish mass; that in the mucous membrane was nearly as soft; the bread in the water less so.

In the second experiment, they had sixty-two grammes (about sixteen drams) of gastric juice. They disposed in separate vessels, 1. gastric juice with raw beef; 2. gastric juice with boiled white of egg; 3. water and beef; 4. water and white of egg; 5. water with ten drops of distilled vinegar and beef; 6. water with the same quantity of vinegar and white of egg. The vessels were kept during the period of ten hours at the same temperature as in the former experiment. The meat macerated in the gastric juice was then found of a pale red, and very much softened on its surface,—a pulpy matter could be scraped from it; the white of egg in the gastric juice was likewise very much softened, and had much the appearance of white of egg from the stomach of a dog which had been fed with it. The meat in the water was whitish and firm; the white of egg also which had been macerated in water only, was quite solid. The substances in the dilute vinegar presented no trace of softening.*

Dr. Beaumont's experiments on artificial digestion are of extraordinary interest. They demonstrate most satisfactorily that the stomach secretes a fluid which has the power of dissolving articles of food even out of the animal body.† As an example, we may instance the 2nd experiment in the 1st series. Dr. Beaumont having, after the boy St. Martin had fasted seventeen hours, obtained from his stomach, by the method

* Tiedemann and Gmelin, loc. cit.

† [The translator has omitted the details of many of Dr. Beaumont's experiments, stating merely the results which they afforded.]

which we have already mentioned, one ounce of gastric juice, put into it a solid piece of recently boiled beef weighing three drams, and placed the vessel which contained them in a water-bath heated to 100°. In forty minutes digestion had commenced on the surface of the meat; in fifty minutes, the fluid was quite opaque and cloudy, the external texture began to separate and become loose; in sixty minutes chyme began to form. At 1 p. m. (two hours after the commencement of the experiment) the cellular texture was destroyed, the muscular fibres loose and floating about in fine small threads very tender and soft. In six hours they were nearly all digested,—a few fibres only remaining. After the lapse of ten hours, every part of the meat was completely digested. The gastric juice, which was at first transparent, was now about the colour of whey, and deposited a fine sediment. A similar piece of beef was, at the time of the commencement of this experiment, suspended in the stomach by means of a thread; at the expiration of the first hour it was changed in about the same degree as the meat digested artificially; but at the end of the second hour it was completely digested and gone.

In other experiments Dr. Beaumont withdrew through the opening into the stomach some of the food which had been taken twenty minutes previously, and which was completely mixed with the gastric juice. He continued the digestion, which had already commenced, by means of artificial heat in a water-bath. In a few hours the food thus treated was completely chymified; the artificial seemed to be but little slower than the natural digestion. (See expts. 25, 26 and 27, second series.)

Several of Dr. Beaumont's experiments,—we may mention expt. 31, second series, and expts. 28, 33 and 48, third series,—demonstrate the influence of temperature, and of the quantity of the gastric juice, on digestion. Experiment 31 of the second series, which with many others contrasts the action of water, with that of the gastric juice on organic substances, may serve as an example. Having obtained from the stomach of St. Martin two ounces of gastric juice, he divided this quantity into two equal portions, and laid in each an equal quantity of masticated roast-beef. One he placed in a water-bath at the temperature of 99° Fahr. and left the other exposed to the open air at a temperature of 34° Fahr. A third similar portion of meat he kept in a phial with an ounce of cold water. An hour after the commencement of the experiment, St. Martin had finished his breakfast, which consisted of the same meat, with biscuit, butter and coffee. Two hours after the meat had been put into the phials, the portion in the warm gastric juice was as far advanced towards chymification as the food in the stomach; the meat in the cold gastric juice was less acted on, and that in the cold water was merely a little macerated. In two hours and forty-five minutes from the time that the experiment was begun, the food in the stomach was com-

pletely digested, the stomach empty, while even at the end of six hours the meat in the gastric juice was only half digested. Dr. Beaumont therefore, having procured twelve drams of fresh gastric juice, added now a portion to each of the phials containing meat and gastric juice, and to a portion of the half-digested food which he had withdrawn from the stomach two hours after the commencement of the experiment, and which had not advanced towards solution. After eight hours' maceration, the portions of meat in the cold gastric juice and in the cold water were little changed; but, from the time of the addition of the fresh gastric juice, digestion went on rapidly in the other phials which were kept at the proper heat; and at the end of twenty-four hours the meat which had been withdrawn from the stomach after digestion had commenced was, with the exception of a piece of meat which had not been masticated, converted into a thickish pulpy mass of a reddish brown colour: the meat in the warm gastric juice was also digested, though less perfectly; while that in the cold gastric juice was scarcely more acted on than the meat in the water, which was merely macerated. Dr. Beaumont now exposed these two phials containing the meat in cold gastric juice and meat in water to the heat of the water-bath for twenty-four hours, and the gastric juice which, when cold, had no action on the meat, now dissolved it; while the meat in the water underwent no change, except that, towards the end of the experiment, putrefaction commenced.

The 48th expt. third series, illustrates the antiseptic power of the gastric juice. A piece of meat which had been macerated at the temperature of digestion in water for several days till it acquired a strong putrid odour, on the addition of some fresh gastric juice, lost all signs of putrefaction, and soon began to be digested and chymified.

To justify our confidence in Dr. Beaumont's statements, we may mention that he always relates the accidental circumstances which occurred in the experiments, and refers to several other physicians, Silliman, Knight, Yves, Hubbard, Dunglison, Sewall, Jones, and Henderson, having interested themselves in them. It must therefore be regarded as an indubitable fact, that the gastric juice is really a solvent for organic substances, both in the stomach and out of the body.*

3. *Are the solvent principles in the gastric juice acids, or other unknown substances?*

* We can therefore be no longer surprised that the stomach is sometimes found to undergo softening sooner than other parts of the body after death, it being acted on by the solvent gastric juice. The phenomenon has been observed more particularly in rabbits and in children, and has by many been attributed to putrefaction. (See Rudolphi's Physiol. ii. 2. 119.) I have observed it in rabbits, and know that in them it did not depend on the mode of death. It is certainly owing to a decomposition, of which, however, the cause must be local and "material," and probably is no other than the chemical action of the gastric juice.

Tiedemann and Gmelin were inclined in favour of the theory which supposes the solution of the food in the stomach to be owing to the action of the acids contained in the gastric juice,—namely, of the acetic and muriatic acids.

For the purpose of ascertaining the degree of solvent action exerted by the acids of the stomach on some organic matters which are not soluble in water, they submitted to the action of these acids at a temperature of about 50° Fahr. during some weeks the following substances: 1. fibrin from the blood of calves; 2. fibrin from the blood of the ox; 3. fibrin from the blood of the horse; 4. the coats of the large venous trunks of the horse; 5. the coats of the larger arterial trunks of the same animal; 6. the white of a hen's egg boiled hard; 7. mucus from the small intestine of a dog; 8. mucus from the small intestine of a horse. The proportions of the fluid and the solid substance, which was weighed in the moist state, the temperature, and the duration of the experiment, were in each case the same.

Acetic acid was completely absorbed by the substances 1, 2 and 4; these swelled up and became each a transparent mass, which, when heated with a fresh portion of acid, was completely dissolved. A small quantity of the acid digested with each of the substances 3, 5, and 6, remained unabsorbed, and afforded a copious precipitate with tincture of galls and ferro-prussiate of potash. The remaining masses of 3 and 5 were swollen, and, on being heated with a fresh portion of acid, became more gelatinous, and were for the most part dissolved. The substance 6 was less swollen, and underwent less change when heated. The mucus, 7 and 8, remained nearly unchanged, and the acetic acid in which it had been macerated did not become turbid on the addition of tincture of galls; but, on being heated with fresh acetic acid, the mucus was nearly wholly dissolved.

The *muriatic acid* had, without the application of heat, dissolved a great part of the substances 1—6, judging by the abundance of the precipitate produced by the addition of tincture of galls; of the mucus, on the contrary, it had dissolved very little.

Dr. Beaumont, likewise, has instituted several experiments with a view to determine the power of acids in dissolving articles of food; and the results which he obtained, although they varied somewhat according to the substances employed in the experiments, have nevertheless led him to the conclusion that no other fluid produces the same effect on food which the gastric juice does, and that *it* is the only solvent of aliment.

He found that common vinegar exerts no more action than water on white of egg digested in them and kept warm in the axillæ; even after five hours' maceration, scarcely any diminution of weight had taken place: while a similar portion of the same substance submitted during

the same period of time to the action of an equal quantity of gastric juice, under exactly the same circumstances, was completely dissolved. (Expt. 46, 4th series.)

Dr. Beaumont made a mixture of muriatic and acetic acids, each diluted to the same degree of acidity as the gastric juice, (judging of this by the taste,) in the proportion of three parts of the dilute muriatic acid, and one part of dilute acetic acid, and compared the action of this fluid with that of an equal quantity of gastric juice from the stomach of St. Martin on different substances, both menstrua being kept at the proper temperature for digestion.

Roast beef, cut small, was in $6\frac{3}{4}$ hours nearly entirely dissolved by the gastric juice, while in the mixed acid it merely lost its fibrous appearance and became a gelatinous mass. After the digestion had been continued eight hours longer, the acids had dissolved all the meat, with the exception of a small portion of gelatinous substance which remained on the filter; but the solution, instead of being a turbid whitish grey fluid depositing a brown sediment on standing like the product of digestion in the gastric juice, was of a reddish brown colour and yielded no sediment. The action of infusion of galls on the two fluids was very different. (Expt. 115, 3rd series.)

There was the same difference in the time required for the solution, and in the products of the digestion, of boiled beef coarsely masticated, in the acids, and in gastric juice. (Expt. 104, 3rd series.)

Isinglass appeared to be more soluble than meat in the mixed acids, but it was nevertheless not so soluble in them as in gastric juice; and the resulting fluid differed from the solution of the same substance in gastric juice, although the differences were less marked in some experiments than in others. (Expts. 105 and 106.)

Saliva acidulated with acetic, or with muriatic acid, so as to resemble in taste the gastric juice, did not possess the solvent properties of the latter fluid. (Expt. 96.)

I had myself long since instituted some experiments with the view to determine whether the theory that the acids are the solvent principles of the gastric juice be correct. I placed small pieces of meat of some grains in weight, and small cubes of coagulated white of egg, in equal quantities of very much diluted muriatic, acetic, tartaric, and oxalic acids; and although after maceration for a short time a precipitate or turbidity could be produced in the liquid by ordinary re-agents, showing that a part of the substances had been dissolved, yet I found the masses of meat and albumen by no means perceptibly changed, even after the lapse of several days;—indeed, the small cubes of coagulated white of egg preserved their angles and edges for weeks. The action was not much greater when the maceration was performed at the heat of natural digestion. Of all the acids of which I tried the solvent power, and

which I have named above, the oxalic, which is known to be poisonous to the human body even in small doses, appeared to have the most powerful action on the substances submitted to it; the fluid became turbid in a short time, and deposited a scanty whitish sediment; but the portions of meat and albumen gave evidence nevertheless of no particular change. At the same time that I was making these experiments, I exposed a glass containing dilute acetic acid and small pieces of meat, during the space of twenty-four hours, to the current of a powerful galvanic battery; I made a similar experiment with solution of common salt; but in neither case was the solution of the organic substance in any perceptible degree accelerated.

The acids which are such powerful solvents for mineral substances, are extremely feeble in their action on organic matters; and if we only remember that dilute or even concentrated acids are inadequate to dissolve completely a small piece of meat or white of egg of the weight of a few grains, though their action is continued for several days, the theory apparently so simple which ascribes the solution of the food to the agency of the acids of the stomach, will cease to appear probable, which it never could do to those who reflected how frequently indigestion is attended with increased secretion of acid. It must, therefore, be allowed that no investigations thus far have informed us of the nature of the active solvent principle of the gastric juice. Berzelius long since made this confession. Everything tended to convince us that the active principle of the gastric juice is an organic substance, of which the action is similar to that of "Diastase" on starch. Such was the state of our knowledge on the subject of digestion before the recent important discoveries of Eberle and Schwann.

Nature of the digestive principle. — Eberle* discovered that, although neither dilute acids nor mucus alone possess the property of dissolving rapidly organic substances submitted to their action, yet mucus mixed with acids has this solvent power; and that albumen or meat digested with acidulated mucus, or with an infusion of mucous membrane in dilute acid, are not merely quickly dissolved, but also undergo a chemical change, the albumen losing its property of coagulability and being converted into osmazome and salivary matter.

The experiments of Eberle have been repeated by Schwann and myself,† and by many others, and have been found in the main quite correct. But Eberle was in error in his statement that all mucus in an acid state has the property which is possessed by an organic principle secreted with the gastric mucus only; the mucus of other organs, — the mucous membrane of the bladder, for example, according to Schwann, treated with muriatic acid, exerts no solvent power. The infusion of the mucous

* Physiologie der Verdauung. Würzburg, 1834.

† Müller's Archiv 1836, p. 68.

membrane of the fourth stomach of the calf in dilute acid affords a digestive fluid; the mucous membrane being dissected from the other coats, washed with cold water until it no longer gives evidence of containing a free acid, and then dried, can in that state be preserved, and is at all times ready for use in experiments.

The principal phenomena of artificial digestion may be demonstrated in a simple manner by the following experiment. The dried mucous membrane is cut into pieces, some of these placed in each of five test tubes, and distilled water poured over them. To the contents of two of the tubes, six or eight drops of muriatic acid are added; to two others, twelve or fourteen drops of acetic acid. The mucous membrane and water in the fifth glass are left without any addition of acid; and in a sixth is placed the same quantity of water with eight drops of muriatic acid, but no mucous membrane. Small cubes of coagulated white of egg and boiled meat of several grains' weight are then placed in each of the tubes. After digestion for twelve hours at a temperature of about 99½° Fahr., the pieces of meat and white of egg present the following appearances. Those macerated in the dilute acid without mucous membrane, or in the water with mucous membrane, but without acid, are unchanged; and the substances in the water alone give out after a time a putrid odour. The pieces of meat and albumen in the acid infusion of mucous membrane are, on the contrary, softened. The coagulated albumen is become transparent, cheesy in the centre, and breaks down easily under pressure. If the digestion is continued for twenty-four hours, the substances in the acid infusion of mucous membrane are dissolved either entirely, or in greater part; and the fluid acquires a peculiar odour, not of a putrescent character, but similar to that of soldier's bread; its taste is acid, and not agreeable. (The fibrin of the blood likewise dissolves very quickly.) The ordinary temperature of the atmosphere in summer is sufficiently high for the success of the experiment; the surface of the masses of coagulated albumen becomes transparent even in a few hours, and becomes surrounded by a cloud of the particles of albumen, which are for the most part in solution. The albumen which has been dissolved by the digestive fluid has lost all its former characters, it is no longer coagulable; and the solution contains osmazome and salivary matter, and, according to Schwann, a third substance similar to albumen, which is precipitated by carbonate of soda, is insoluble in water and alcohol, and soluble in dilute muriatic and acetic acids. This third substance is moreover precipitated neither by the boiling temperature, by acetate of lead, nor by alcohol; but is thrown down in large quantity by nitric acid, and oxymuriate of mercury, and less copiously by cyanuret of iron and potassium, and by tincture of galls.

We found that neither carbonic acid is evolved nor oxygen gas ab-

sorbed during the artificial digestion, in both which circumstances it differs from the fermentative process.*

The experiments of Eberle, and those instituted by Schwann and myself, still left it uncertain whether the digestive principle in an undissolved state acts by the influence of contact, or whether it is itself in solution and acts by dissolving the organic substances. Schwann,† however, has discovered that the infusion of mucous membrane with dilute acid, even after it is filtered, still retains its digestive power. The digestive principle, therefore, is clearly in solution, and the theory of digestion by contact falls to the ground. The clear filtered fluid has the colour of saturated urine; it retains its solvent property for months. The proportion of acid recommended by Schwann for the preparation of the digestive fluid, is 3·3 grains to half a loth (about a quarter of an ounce) of the mixture of mucous membrane and water. If the proportion of the acid remains the same, the quantity of the fluid as compared with that of the membrane is not of much importance; the quantity of the water may be twice or five times that of the mucous membrane in its moist state.

Schwann has performed several experiments to determine the part which the acid plays in the digestive fluid. The experiments already detailed prove that the acids are necessary; but it was possible that they might merely serve for the production of the digestive principle, and might, after this was formed, be no longer essential. This, however, is not the case; the digestive fluid when neutralised with carbonate of potash was inert, but recovered its power on the addition of the proper quantity of muriatic acid. To ascertain whether the acid acts the part of a mere solvent of the digestive principle, Schwann added to some of the fluid as much carbonate of potash as neutralised more than half the acid of the fluid, which was still acid, and remained clear and without sediment; so that the digestive principle could not have been precipitated, and yet the solvent power of the fluid was lost. The acid therefore is more than a mere solvent of the active principle. It still appeared possible that the acid might enter into a chemical combination with the digestive principle, forming a compound similar to the acid salts. But if such were the case, the quantity of acid necessary ought to be regulated by the quantity of the organic digestive principle; and Schwann found that it is not so: on the contrary, the quantity of the acid bears no relation to the quantity of the organic digestive principle, but is regulated by the quantity of the fluid. Again, the acids do not serve simply to dissolve the products of digestion; for although these are soluble in acids, and even in very dilute acids,

* Müller und Schwann, loc. cit.

† Müller's Archiv. 1836, p. 90. Schwann, über das Wesen des Verdauungs processes.

yet a quantity of the digestive fluid which is adequate to the solution of a certain quantity of albumen, loses its solvent power when diluted. Lastly, if it was the part of the acids to enter into combination with the products of digestion during their formation, the proportion of the acids in the fluid ought to become less as the digestion advances; but their proportion undergoes no change. Dr. Schwann infers, therefore, that the dilute acids, without themselves undergoing any change, aid by their presence in effecting the decomposition of the organic substances, just as they aid in the conversion of starch into sugar when boiled with it.

The artificial digestion by means of the acid infusion of gastric mucous membrane may be compared with fermentation, and with the cases of decomposition by contact, inasmuch as both in it, and in these processes, a very small quantity of the decomposing agent is sufficient to produce the effect,*—namely, a spontaneous decomposition. It results also, from Schwann's observations, that the digestive fluid loses a part of its power during its action, which does not, however, give rise to the production of new active principle, and thus differs from the process of fermentation. Moreover, no carbonic acid is developed during artificial digestion, and not the smallest quantity of oxygen is necessary to the process, as Schwann has proved by accurate experiments. Many substances which disturb the progress of the vinous fermentation, likewise interfere with digestion; thus, as Schwann shows, alcohol and the boiling temperature render the digestive principle inert; the same is the action, in a less degree, of the neutral salts, and particularly of the sulphites. But arseniate of potash, which puts a stop to the vinous fermentation, was found by Dr. Schwann not to disturb the artificial digestive process.

Chemical properties of the digestive principle.—It must be almost impossible to obtain the solvent principle of the digestive fluid in a separate state, on account of its active property being so easily destroyed by re-agents. Several of Schwann's experiments show the action of different substances upon it. It is not precipitated when the acid of the mixture is neutralised; on the contrary, it is soluble in water alone; it is precipitated from the neutral solution by acetate of lead, and can be obtained again in an active state from the precipitate by means of hydro-sulphuric acid. Ferro-cyanuret of potassium, as well as ferro-cyanide of potassium, produce a precipitate in the acid solution of the digestive principle, but none in the neutral solution; but the precipitates which they throw down do not contain the digestive principle; the fluid retains its solvent property. Corrosive sublimate produces a precipitate both in the acid and in the neutral fluid. Tannin throws down a precipitate, alcohol and the boiling heat cause turbidity, and all three render the fluid inert. The solvents of the digestive principle are

* 4·8 grains of digestive fluid, or 0·11 grains of dry residue of the fluid, were sufficient when diluted for the solution of 60 grains of moist albumen.

water, and dilute muriatic and acetic acids. These characters, as well as its peculiar action on casein, justify us in regarding the digestive principle as a peculiar substance, to which, although we cannot procure it in a separate state, we may, on account of its properties, give the name of "pepsin."

The action of the digestive principle on casein deserves a more particular consideration. Berzelius had already pointed out that the rennet of the calf has the property of coagulating milk even after all traces of acidity have been removed by washing. It is known, too, that the coagulation of the casein produced by rennet is peculiar, inasmuch as the curds are insoluble in water, while the coagula of casein produced by alcohol or acids are again soluble in water, and in an additional quantity of acid. Now Schwann has shown that this property of coagulating the casein is possessed by the artificial digestive fluid even when neutralised. On the addition of a very small quantity of the acid fluid to milk, and the application of heat, the coagulated casein soon separates: of the neutral fluid, more than 0·42 per cent. are necessary; 0·83 is sufficient. The power of the artificial digestive fluid to coagulate milk is destroyed by the boiling temperature; it cannot, therefore, be the saline ingredients which produce the coagulation. This peculiar action of the digestive principle on milk renders the latter fluid a test for its presence; if a neutral fluid coagulates milk, but loses this property immediately on being boiled, we may infer that it contains the digestive principle. Schwann has in this way proved that the digestive principle which we are here considering, really exists in the stomach. He divided the stomach of a rabbit, which had died immediately after birth, into two portions; boiled one, and then added to each some milk. On the application of a gentle heat, the milk coagulated in the portion which had not been boiled, while in the other it remained unchanged.

The solution of some of the alimentary substances is effected not by the digestive principle which we have named pepsin, bnt by the acids, either principally, or with the aid of another organic matter.—The substances easily soluble in the digestive principle are fibrin, muscular substance, and coagulated albumen; while casein, gelatin, and vegetable gluten appear, from Schwann's experiments, not to be dissolved by it. For when they were digested separately with diluted acids and dilute digestive fluid, no difference could be perceived in the change which they underwent in the two fluids; while the fluids resulting from the digestion of these substances in the mere dilute acids, displayed the same characters with re-agents as were observed by Tiedemann and Gmelin in the products of the solution of the same substances in natural digestion, with the exception of those due to the starch, which was absent here. The gelatin lost its property of coagulating; and tincture of iodine threw down a precipitate in the solution of gluten in the dilute acid, but produced no change of colour.

The action of an acid is not adequate to explain the changes which starch undergoes in natural digestion, namely, its conversion into gum of starch and sugar. The digestion of starch in dilute acid, even with the addition of some of the artificial digestive fluid, does not give rise to the formation of any sugar. But Schwann has found correct the statement of Leuchs that starch is converted into sugar by the action of saliva. He digested in some acidulated saliva for twenty-four hours a certain quantity of boiled starch, then filtered the fluid, and found that iodine produced in it no change of colour. Having neutralised it, and evaporated it to dryness, he obtained from the residue by means of alcohol a considerable quantity of sugar, which he recognised by its taste as well as by its property of fermenting with yeast. The part of the residue which the alcohol did not take up consisted of the salivary matter of the saliva in part altered in its properties, and starch changed to a substance resembling gum, which did not with iodine strike the colour which characterises starch.*

Since the activity of the digestive principle depends on the presence of a free acid, it is easy to understand how a neutral gastric fluid holding saline matters in solution can, as Purkinje has observed, be again rendered active by the agency of galvanism, which will decompose the salts, free acid collecting at the positive pole.

Influence of the nerves and electricity on digestion.—It has indeed been supposed that electricity is capable of replacing the influence of the nervus vagus in digestion when this influence has been lost. The digestive process is nearly entirely arrested by the division of the vagus nerves on both sides.† Blainville, having performed the experiment on pigeons, observed that the vetches which they swallowed afterwards remained unaltered in their crop, and that the process of chymification was wholly arrested. The same result attended similar experiments by Legallois, Dupuy, Dr. Wilson Philip, Clarke, Abel, and Hastings. While, on the other hand, Broughton, Magendie, Leuret, and Lassaigne state that digestion appeared to them to be uninfluenced by the division of the nerve in question. Mayer‡ also has observed that the digestive process continued for a certain time, and that acid chyme was formed at all events in rabbits. Brachet,§ too, states, that in all his experiments the food underwent chymification at the parts where it was in contact with the coats of the stomach.

The question cannot, however, be determined with complete certainty in quadrupeds, on account of death taking place so quickly in them in consequence of the operation; I have therefore, in conjunction with Dr. Dieckhof, instituted experiments on birds, particularly geese; after the birds had been forty-eight hours without food, they were fed with

* Schwann, loc. cit. † See page 355. ‡ Tiedemann's Zeitschrift, ii. 1.
§ Recherches sur les fonct. du Syst. Gangl. Paris, 1830.

oats. In each experiment two birds were required. In one the vagus was divided on both sides, the other was left uninjured for the sake of comparison. After the death of the first, which took place in the space of five days, the second was killed. In the latter the crop was generally empty; in the former it was always fully distended with oats, and some grains were contained in the muscular gizzard, and these were in part crushed. The fluid in the stomach was acid, but less so than in the other uninjured animal. Hence we may conclude that digestion is for the most part, but not entirely, checked by the division of the nervi vagi. Tiedemann states, it is true, that after both vagi had been divided in a dog, neither the matter vomited nor the mucus secreted by the stomach was acid; and Mayer also relates that in his experiments on cats and dogs the chyme formed after the operation was not acid: yet he found the chyme acid in rabbits; and in my experiments with Dr. Dieckhof I never found the acidity absent, although it was less marked than in the sound animal.

Dr. Wilson Philip has asserted that, after the experiment of dividing the nervi vagi has been performed, the digestive action may be restored by means of an electric current transmitted through the vagus nerve, one pole of the battery being applied to the nerve, the other to a piece of tin foil laid over the epigastric region. The experiments were repeated by Breschet and Vavasseur. They found that simple division of the nervi vagi had not the effect of completely arresting the digestive process, although this was the result when the nerve was not merely divided, but a portion removed.* I must remark, however, that when a nerve is divided, whether a portion is cut out or not, it is paralysed, and remains so for a very long time. Breschet and Vavasseur in the next place affirmed, that by directing an electric current through the divided nerves, digestion could be entirely restored; in which effect they attribute some share to the increased muscular action of the stomach. Breschet and Edwards† have, however, since modified these views: as the results of their later experiments, they announce that division of the nervi vagi retards chymification, but does not completely arrest it; that this retardation of the process depends on the paralysis of the œsophagus, which is likewise the cause of the vomiting that occurs after the operation; and that the restoration of the digestive process by means of the electric current is not owing to the electricity itself, but to the irritation of the vagus nerve produced by it, since mechanical irritation of the lower portion of the nerve has the same effect in restoring the digestive process, which it does by re-exciting the motions of the stomach. But as I have frequently stated, on the ground of experiment, the motions of the stomach cannot be in the slightest degree affected by irritation of the nervus vagus. If MM. Breschet and Edwards had

* Froriep's Notiz. vi. 261.

† Arch. Gén. de Med. 1828.

only continued their experiments longer, they would perhaps have perceived that neither the electric nor mechanical stimulus had any remarkable effect on the digestive process; that the animals remained in the same state, whether these stimuli were applied or not, as appeared to be the case in the following experiments of Dr. Dieckhof and myself.

In each experiment we took three rabbits, kept them without food for forty-eight hours, and then fed them with cabbage. One was left uninjured; in the second the two nervi vagi were simply divided; and in the third the nerves were in like manner divided, but in it a galvanic current was directed through the nerves in the way directed by Dr. W. Philip, and maintained for seven or eight hours. As soon as either the third or the second rabbit died, the other two were also killed. In every experiment we found that the sound rabbit had digested perfectly; all that remained of the food was the insoluble portion, which was nearly dry; in the two others the food in the stomach was in nearly exactly the same state in both: in one instance the food of the rabbit in which the galvanism had been applied was somewhat less digested; in many cases the state of the food in the two was exactly the same, and in several instances it was in the galvanised rabbit perhaps somewhat less digested than in the other, but the difference was scarcely to be noticed.*

Matteuci affirms that he has been able to effect the artificial digestion of meat with chloride of sodium and the simultaneous influence of electricity. Grounding his opinion on the experiments of Wilson Philip, Matteuci imagines the acid reaction of the stomach to be produced by a positive electric state of the viscus. To prove this he took a piece of boiled meat, poured over it water, and added some common salt and carbonate of soda; he kept the mixture a long time at a proper temperature, constantly triturating it until it was reduced to a pulpy mass like that produced by mastication. He then introduced the pulp thus prepared into a bladder moistened with solution of common salt, and connected with the bladder the pole of a galvanic battery of eighteen or twenty pairs of plates. He states that now along the walls of the bladder, and especially around the positive wire, a layer of a whitish dense substance full of bubbles of oxygen gas was formed; that this substance was flaky, and after being dissolved in water coagulated when heated. I had during a very long period tried in vain to dissolve portions of meat in acids or chloride of sodium with the aid of an electric current; the results obtained by M. Matteuci could not, therefore, but appear very improbable to me. I have, in conjunction with Dr. Dieckhof, repeated the experiment; we introduced into different bladders two portions of the same pulp, consisting of

* Dieckhof de actione quam nervus vagus in digestionem ciborum exerceat. Berol. 1835.

pieces of meat with common salt and carbonate of soda; one bladder only was subjected to galvanism, the other was left undisturbed. At the conclusion of the experiment no kind of difference could be detected between the fluids contained in the two bladders.

c. *Of the changes which the chyme undergoes in the small intestine.*—We recur to the excellent researches of Tiedemann and Gmelin, for they contain all we know with certainty relative to the subsequent changes which the chyme undergoes. In the duodenum the chyme is acid. The stimulus which it exerts on the coats of the intestine, and which is propagated along the ductus choledochus and its branches generally, gives rise to the effusion of bile and pancreatic juice; Tiedemann has at least found the gall bladder almost empty in animals in which digestion was going on. After gelatin had been given as food, it could still be detected in the contents of the small intestine; when butter had been given, the contents of the small intestine contained a fatty matter; casein was detected, though not distinctly, when the animal had been fed with cheese; and some remains of starch were found, though not always; the starch was in greater part converted into gum of starch. When the food had consisted of milk, cheesy clots were met with in the first half of the small intestine. A dog having been fed with some bones, small fragments of the bone were found in the upper half of the small intestine; in the lower half, abundance of phosphate of lime, with a small quantity of carbonate of lime. In horses which had been fed on oats the upper half of the small intestine still contained starch, but in the middle and lower part of the intestine this substance had no longer its characteristic properties.

Tiedemann and Gmelin found the contents of the upper half of the small intestines acid, though less strongly so than the matters in the stomach; the acidity gradually diminished in approaching the cæcum, and at the extremity of the ilium could usually be no longer detected. The experiments of these observers leave undetermined the cause of the chyme losing its acidity,—whether it is owing to its acid being neutralised by the alkaline carbonate of the bile, or to the lower part of the small intestine pouring out an alkaline secretion; or whether, in consequence of decomposition commencing, ammonia is developed and neutralises the acid; or lastly, whether the acid part of the chyme is absorbed from the intestines, in which case it must lose its acidity in its course through the lacteals and mesenteric gland, since the chyle itself is certainly alkaline.

The principal animal matters composing the chyme of the small intestines are:

1. Albumen; of which the quantity decreases in the lower part of the small intestines in consequence of the absorption of the chyme by the lacteals.

2. Casein; which likewise diminishes in quantity as we approach the cæcum.

Respecting these two substances, it cannot be determined how large a share of them is owing to digestion, how much to the secretions poured into the digestive canal,—for instance the pancreatic secretion. Tiedemann and Gmelin think it possible that the casein of the pancreatic secretion containing a large proportion of nitrogen yields a portion of this element to different ingredients of the alimentary substances, which contain less nitrogen, so as to reduce itself to their standard in this respect, and to convert them into albumen.

3. An azotized substance precipitated by muriate of tin. (Salivin and osmazome?) Its quantity diminishes in the course of the matters through the small intestines.

4. A matter to which chlorine imparts a red colour,—derived probably from the pancreatic secretion, since it cannot be detected in the stomach; and is found in the small intestines after the bile duct has been tied, and cannot therefore be derived from the bile. It is not found in the matter of the excrement.

5. Substances soluble in alcohol, and insoluble in water. Fatty matter, stearine and the colouring and resinous matters of the bile.

The substances here enumerated do not differ in their nature from those which Tiedemann and Gmelin found in the contents of the intestines in animals which had been kept without food. With the exception, therefore, of the abundant albumen, the product of the food, they are most probably derived from the secretions poured into the canal, particularly the pancreatic secretion, which contains albumen, casein, and a matter which is reddened by the action of chlorine.

Influence of the biliary secretion on the chyme.—Dr. Beaumont has investigated by experiment the effect of mixing bile with the chyme out of the body. On adding some bile of the ox to chyme obtained from the stomach of St. Martin, a turbid yellowish-white fluid, or rather delicate white coagula were formed, which, after standing some little time, separated into bright yellow flakes, which sank to the bottom of the vessel, and a turbid milky fluid. For the sake of comparison, Dr. Beaumont mixed, in another experiment, bile and dilute muriatic acid, of each one drachm, with two ounces of water; and a similar turbidity was the result; but the sediment which formed was gelatinous and of a deep green colour, and the remaining fluid of a blueish-green colour, and not milky as in the former case.

Purkinje has observed that the addition of even a small quantity of bile to the digestive fluid puts a stop to artificial digestion. Tiedemann's and Gmelin's researches afford no satisfactory information relative to the office of the bile in the process of chymification. The acids of the

chyme coagulate the mucus of the bile and precipitate it, together with a great part of the colouring matter. The cholesterine, likewise, is precipitated, and is obtained by digesting in alcohol the part of the contents of the intestine which is insoluble in water. The margaric acid found in the contents of the small intestines is believed by Tiedemann and Gmelin to be likewise derived from the bile. The portion of the intestinal contents which is insoluble in water, contained the resin of the bile, which appeared to them to be an excrementitious substance, having no influence in the changes which the food undergoes, and a principal ingredient in the fæcal matter. The opinion of Werner,* which is generally adopted by physiologists,—namely, that the chyle is precipitated by the bile in the form of flocculi,—was found by Tiedemann and Gmelin to be groundless. The mixture of bile with the fluid contents of the stomach produced no other precipitates than resulted from the addition of an acid to bile. The flocculi in the small intestine, which are supposed to be flakes of chyle, are nothing more than shreds of mucus, and were present even when the ductus choledochus communis had been tied. The chyle which is absorbed by the lacteals is fluid. Autenrieth and Sir A. Cooper speak of the chyle as a tolerably consistent matter lying between the villi, which coagulates when exposed to the air.† This matter is, however, according to Tiedemann and Gmelin, merely mucus; its coagulation, therefore, must be a mistake. The matters in the bile which have a share in producing the necessary changes in the chyme, are probably the picromel, the osmazome, the matter similar to gliadin, and the cholic acid, since it appears from the investigations of Tiedemann and Gmelin that they do not exist in the excrement. It is not probable that the sole office of the bile in addition to the elimination of the resin and colouring matter, which are excrementitious substances, is to neutralise the acid of the chyme, and thus to prepare the latter for the change which it undergoes in the lacteals, where in the state of chyle it becomes alkaline. Those of its essential components which do not form part of the excrement, either contribute to complete the solution of the chyme, which was Haller's opinion; or they must serve to effect the conversion of the chyme into the chyle,—that is to say, the production of albumen from the food, as Prout supposes. The chyle taken from the lacteals contains, with the exception of albumen, none of the animal matters which Tiedemann and Gmelin detected in the intestines, nor those soluble components of the bile which do not form part of the excrement; all that the chyle contains in place of these matters is albumen.

* Exp. circa modum, quo chymus in chylum mutatur, Diss. Inaug. præs. Autenrieth. Tub. 1800.

† See also Abernethy's Physiol. Lectures, p. 189.

Effects of ligature of the bile duct.—Sir B. Brodie* has endeavoured to ascertain the degree in which the bile contributes to the process of chylification, by applying a ligature to the ductus choledochus. Jaundice was a consequence of the operation, but this sometimes disappeared after a time; and then it was found that an effusion of lymph had taken place at the seat of the ligature, and reunited the divided portions. As to the effect of the operation on digestion, Sir B. Brodie states that the process in the stomach was unaffected, but that chyle was no longer formed from the chyme; that neither the lacteals nor the thoracic duct contained any white chyle.

Tiedemann and Gmelin have rendered valuable service to physiology by the experiments (ten in number) which they have performed to ascertain the correctness of Brodie's statement. The results which they obtained are the following: jaundice ensued on the second or third day after the operation, but disappeared again in some instances after the lapse of ten or fifteen days, the canal of the duct being in such cases restored by a spontaneous process; either the ligature had cut through the coats and fallen away before the divided ends of the duct united, or, lymph having been effused around the ligature, this had separated, and fallen into the cavity of the duct thus restored on the exterior, and was subsequently carried out through the duct. After an interval varying from thirteen to twenty-six days, the canal was found to be restored. In other cases (experiments 1, 4, and 8) death ensued at the end of from three to seven days. One dog, in which the jaundice continued although the duct was afterwards found pervious, had lived twenty-six days after the operation, when he was killed. In one case (experiment 1), in which the dog died seven days after the duct had been tied, the animal had become so emaciated and feeble that it could scarcely stand. After death they found inflammation of the peritoneum, or some of its effects. The colouring matter of the bile was detected in the blood and urine, and the lymphatics of the liver were yellow. In the experiments of Tiedemann and Gmelin, as in those of Brodie, digestion went on in the stomach uninterruptedly. The contents of the small intestines also did not essentially differ from what they are under ordinary circumstances: they contained albumen in large quantity; the matter which acquires a red colour when acted on by chlorine was also present; but the casein, which perhaps was present, and the matter which is precipitated by muriate of tin, could not be detected, on account of the presence of albumen. In all Tiedemann's and Gmelin's experiments the contents of the large intestine had a much more fetid and disagreeable odour than ordinarily; (while Leuret and Lassaigne stated that they had a strong odour and insipid savour, not the usual disagreeable odour and savour:) the excrements were white. (I have

* Quarterly Journ. of Sc. and Arts, 1823.

observed that of two similar portions of spleen, if the one was macerated in the bile of the ox, the other in the same quantity of water, the latter became putrid somewhat sooner than the first). In dogs which were killed while fasting, the thoracic duct contained a clear, transparent, yellow fluid, which sometimes coagulated but little, sometimes perfectly. In dogs which had been fed after the operation, the lacteals of the small intestine contained a clear, transparent fluid, just as in the dogs which had not taken food; while in dogs in which the ductus choledochus had not been tied, the contents of the lacteals are milky. The fluid of the thoracic duct was generally redder than ordinary, and yielded a larger and redder coagulum in dogs in which the bile duct had been tied than in those in which the operation had not been performed: the serum in the first was yellow and turbid, in the last milky. The nature of the fluid in the thoracic duct does not, however, prove much in reference to the question; for the lymph from other parts of the body is also coagulable, and in animals kept without food the lymph continues to afford a coagulum for a very long time, as Collard de Martigny has shown, and the lacteals in such animals likewise carry lymph. It is, however, a very important fact, that after the ductus choledochus has been tied, although the animals are fed, the chyle is transparent, while in the natural state it is milky. Tiedemann and Gmelin, indeed, do not attribute much weight to this circumstance, and regard it as certain that chyle is still formed without the aid of bile; for, they say, the white milky colour of the chyle is known to be owing to the presence of particles of fat. Still this difference in the appearance of the chyle, after the ligature of the bile duct, deserves further consideration. The experiments of Tiedemann and Gmelin do not prove, in a satisfactory manner, that the formation of chyle is independent of the bile. Tiedemann and Gmelin also urge as an argument in favour of their opinion, that many of the dogs lived for a considerable time after the operation,—from three to seven days. In one case, in which the jaundice remained, although the canal of the duct was restored, the animal lived twenty-six days; at the end of which time it was killed. But dogs will live about thirty-six days, although wholly deprived of food. Leuret and Lassaigne, who, with Tiedemann and Gmelin, maintain that digestion and chylification are not arrested by ligature of the ductus choledochus, attribute to the bile the property of dissolving the fat, of decomposing it, and forming with it a kind of soap, thus effecting its digestion. But experiments of Tiedemann and Gmelin show that bile is not capable of dissolving the smallest quantity of fatty matter, and can therefore contribute to its division and absorption only in a mechanical manner, by effecting its suspension in minute particles.

The bile seems to be a necessary stimulus for the peristaltic motions

of the intestines; for, when its flow is arrested, constipation is the result.

Changes which the ingesta undergo in the large intestine. — The mixture of chyme, mucus, bile, and pancreatic juice, becomes in its passage through the lower part of the small intestines more consistent and of a darker colour. The fluid parts are absorbed by the lacteals. All the solid matters, as mucus, skins of fruit, woody fibre, horny matter, and those ingredients of the bile which are excrementitious, such as the mucus, colouring matter, fatty matter, and resin, on reaching the lower extremity of the small intestine, constitute the excrement, from which, however, the fluid ingredients continue to be absorbed in its passage through the large intestine.

Tiedemann and Gmelin regard the acid secretion of the cæcum as a second solvent of the animal matter. This second digestion would appear to take place principally in the herbivora, in which the cæcum is especially large; and it is very probable that in the horse, in which the food passes the pylorus in a far less perfectly dissolved state, the digestive process must be continued in the very large cæcum and colon. Schultz follows Tiedemann and Gmelin in admitting that digestion is renewed in the cæcum, but supposes that the gastric and cæcal digestions antagonise each other; that the first is performed during the day, the latter during the night, and that the first commences when the latter ceases. Each meal ought, according to this hypothesis, to pass through the whole intestinal canal in twenty-four hours, which is not regularly the case. In Tiedemann's experiments of ligature of the ductus choledochus, the excrements did not appear white until two days after the operation. Schultz imagines, moreover, that while the digestion is going on in the large intestine, the entrance into it is closed, and that bile collects in the lower part of the small intestine, and does not enter the large intestine till chymification in the latter is completed; that it then flows into the cæcum, and neutralises the chyme.

Gaseous matters in the intestines. — Air is swallowed with the food, and is in the stomach partly converted into carbonic acid; but, in addition to this, a development of gas takes place during digestion in the whole extent of the alimentary canal. Its nature depends partly on the kind of food, and partly on the state of the digestive organs. In affections of the nervous system the evolution of gas is often very abundant; it is sometimes devoid of smell, but generally has the odour of sulphuretted hydrogen, and is frequently inflammable. It may consist of hydrogen, carburetted hydrogen, or sulphuretted hydrogen. The analysis of the gases contained in the intestines of executed criminals afforded Magendie and Chevreul the following results:—

The gas in the small intestine consisted, in three individuals, of

Carbonic acid gas	24·39	40·00	25·00
Hydrogen	55·53	51·15	8·40
Nitrogen	20·08	8·85	66 60
	100·00	100·00	100 00

	The gas in the colon consisted of		That in the rectum of
Carbonic acid	43 50	70·00	42·86
Carburetted hydrogen, with traces of sulphuretted hydrogen	5·47	—	—
Hydrogen, and carburetted hydrogen	—	11·60	—
Pure carburetted hydrogen	—	—	11·18
Nitrogen	51·03	18·40	45·96
	100·00	100 00	100·00

I refer to Berzelius* for an account of the composition of the excrement. Human fæces, of consistence sufficient to form a coherent mass, are, according to his analysis, formed of

Water			75·3
Matters soluble in water	Bile	0·9	5·7
	Albumen	0·9	
	Peculiar extractive	2·7	
	Salts	1·2	
Insoluble residue of the food			7·0
Insoluble matters which are added in the intestinal canal,—mucus, biliary resin, fat, and a peculiar animal matter			14·0
			102 0

In birds and reptiles the urine and fæces are both received into the cloaca.

CHAPTER VI.

OF CHYLIFICATION.

During the passage of the chyme through the whole tract of the intestinal canal, its completely digested parts are taken up by the lacteals. The mode in which this absorption is effected has been already discussed at pages 263, 265, and 280, in the section on the lymph and lymphatic vessels. The observation there adduced (page 263), that the serum of the blood of kittens which are sucking is sometimes perfectly white, would make it appear probable that in those cases the globules of the milk did really gain entrance into the lacteals. But this state of the blood is not constant under the circumstances indicated, and it might arise from the same cause as the similar appearance which the blood

* Chimie Animale, p. 268.

sometimes presents in adults, when the chyle has not undergone the change of sanguification, or when it contained a great quantity of fatty particles. The coats of the radicle lacteals must, it is clear, have invisible pores, since they absorb fluids; but these pores, even if they allow the passage of globules, cannot be larger than the chyle globules themselves, which Prevost and Dumas state to have a diameter of $\frac{1}{7199}$ of an inch, and which, according to my measurement, are for the most part (in the calf, goat, and dog) half or one-third the size of the red particles of the blood of a mammiferous animal. For if the size of the pores was more considerable, larger particles of the chyme would enter the lacteals, which is not observed to be the case; once only, namely, in a rabbit, I found the smaller number of the chyle globules larger than the particles of the blood; and once also, namely, in the cat, I found some of them equal in size to the blood particles, but here also the greater number were smaller. The larger particles which I saw in the chyle of the rabbit could not, however, have entered through the coats of the intestinal villi, for openings which would allow their passage must be visible. The large openings called Lieberkuehn's follicles, which are distributed in such numbers over the surface of the mucous membrane between the villi, and which are so distinctly visible, being nearly twelve times larger than the red particles of the blood, are mere crypts, and appear to be in no way connected with the lacteal absorption.

The chyle is the fluid absorbed from the intestines by the lacteals during digestion, and differs from the lymph which these vessels contain at other times, and from the contents of the lymphatics of other parts of the body, in being of a white or milky colour. In birds it is usually not milky, but clear, and it is likewise not very turbid in most of the herbivorous mammalia; but in the carnivora, and even in the young of the herbivora while they are nourished with milk, it is always more or less turbid and whitish. The colour is owing to the presence of globules, the size of which I have stated above. The chyle is very rarely red; it has been seen of this colour only in very few instances, as, for example, in the thoracic duct of the horse: in the animals in which I have examined it—the calf, goat, dog, cat, and rabbit—the chyle has never been otherwise than white, even in the thoracic duct. Chyle has an alkaline reaction, and its smell has by some been compared to that of human semen.

Chyle coagulates spontaneously in a short time after its removal from the vessels. Reuss and Emmert agree with Tiedemann and Gmelin in stating that the coagulability of the chyle increases with its progress through the absorbent system; that the chyle of the lacteals does not coagulate, and indeed has rarely the property of coagulating spontaneously even when it has traversed the mesenteric glands. The chyle of the thoracic duct coagulates, like the lymph, in about ten minutes after it is taken from the vessel, and separates into coagulum and serum. The

coagulum is the fibrin of the chyle mixed with some of the globules. The serum is a solution of albumen, with another portion of the globules suspended. At the same time, a creamy matter, which consists of fatty particles, collects on the surface.

The coagulum of the chyle of the thoracic duct, after exposure to the air, often becomes much more red than it was previously. On comparing the chyle taken from the lacteals themselves, with that from the cysterna chyli, and again with chyle from the middle and upper portions of the thoracic duct, Emmert* found that the action of the air produced little change on the milk-white chyle of the lacteals, while that of the receptaculum chyli acquired a slightly red tint, and yielded a slight coagulum. The chyle again from the upper part of the thoracic duct assumed a tint approaching very nearly that of arterial blood, and separated into serum and a kind of crassamentum, which was more solid and larger than in chyle taken from other parts of the lacteal system. The serum of the chyle from the receptaculum and the great lacteal trunks was less limpid, turbid, and contained a great number of whitish-yellow globules. The serum of the chyle of the thoracic duct was transparent, and to the naked eye appeared to contain no globules. The chyle which Emmert obtained from the middle portion of the thoracic duct contained somewhat more animal matter than that which he took from the upper part of the duct; this may be accounted for, perhaps, by the circumstance that the upper part of the thoracic duct would contain in addition to the chyle a relatively larger proportion of the lymph from other parts of the body, which is a much more diluted fluid.†

Differences in the chyle arising from variety of food.—Magendie states, that chyle derived from food which contains little or no fat, is not so milky, is rather opaline; and that when it separates into coagulum and serum, but little of the cream-like matter rises to the surface. On the contrary, chyle, he says, which is formed from food of a fatty nature, whether it be animal or vegetable, is white, and separates into three substances,—a fibrinous coagulum, serum, and a creamy stratum on the surface of the fluid, which contains the fatty ingredients. Dr. Marcet‡ has observed, that chyle from vegetable food putrefies more slowly than chyle from animal food, and contains more carbon; the chyle from animal substances, he says, is always milky and affords an oily scum, which does not form on the more transparent chyle derived from vegetable diet.

Tiedemann and Gmelin observed that the chyle of sheep fed on grass or straw was very slightly turbid, was nearly clear. The turbidity was very slight likewise in the chyle of dogs which had been fed upon liquid albumen, fibrin, gelatin, cheese, starch, and gluten, as well as in that of

* Scherer's Journal der Chemie, v. p. 164, 691.

† See also Reil's Archiv. viii. 146.

‡ Medico-Chirurg. Trans. 1815.

a horse fed with starch. The chyle of sheep which had eaten oats was moderately turbid. But the chyle of dogs, of which the food had consisted of coagulated albumen, milk, bone, or beef, or that of horses fed upon oats, was very milky. But the whiteness and opacity were most marked in dogs fed on butter.

Nature of the chyle globules, and cause of the white colour.—Tiedemann and Gmelin,—who, on account of the accuracy with which their experiments were performed, and of their having brought both chemistry and anatomical physiology to their aid in conducting them, are looked upon as the highest authorities in every question connected with the subject of digestion,—declare* that the facts which they observed prove indubitably that the milkiness of the chyle is owing to its containing fatty matter suspended in a state of fine division. When the chyle coagulates, a small portion of the fat becomes included in the clot, while the greater part remains suspended in the serum, to the surface of which it sometimes rises like a cream. From the clot they were frequently able to extract a yellowish-brown fat by means of boiling alcohol; and on agitating the serum with ether freed from alcohol, it gradually became transparent, and the ether when evaporated yielded a fatty substance partly solid and partly fluid, (a mixture of stearine and elaine,) the quantity of which was proportionate to the degree of turbidity of the serum. These facts led them to the conclusion that the fat of the body is derived directly from the food, and that in the chyle at least it is not in the state of solution, but merely of minute division, and in this they were further confirmed by the results of their observations above detailed relative to the effect of difference of food on the appearance of the chyle. Ligature of the thoracic duct caused the chyle to be less turbid; and Tiedemann and Gmelin believe that this may be accounted for on the supposition that the minute division of the fatty matter and its suspension in the watery fluid are effected by the bile.

The chyle, however, does not appear to be a mere solution of animal matter, containing no other globules than those of fatty matter. I have before remarked,† that after chyle had been rendered more transparent by the action of ether, I could still, by the use of the microscope, distinguish globules in the turbid matter at the bottom of the fluid. I have too examined with the microscope the milky chyle with which I found the lacteals and thoracic duct of a dog filled, on killing him five hours after he had taken food, consisting of bread, milk, and some butter. In a drop of this chyle I saw numerous globules of oil, very unequal in size and quite transparent; but the greater part of the globules were of quite another kind, namely, whitish, not transparent, very small, about half or two-thirds the size of the particles of the blood of the dog; a difference which I had previously remarked in the calf. These minute

* Recherches sur la Digestion, Part ii. p. 72.

† See page 262.

globules, which are smaller than those which I and Dr. H. Nasse observed in human lymph, and are less regular in form than the red particles of the blood, are excessively numerous, and are evidently the cause of the white colour of the chyle. Having diluted a small quantity of the chyle with water, that the globules might be seen more distinctly by being less closely aggregated together, I watched its coagulation under the microscope, and could perceive that the change did not consist in the aggregation of the globules, but that, exactly as in the case of the lymph or blood, the delicate pellicle or clot which formed was constituted in great part by a transparent substance which connected together the globules, even though these were widely separated. But, in addition to the delicate pellicles which were thus evidently owing to the coagulation of animal matter previously in solution, there formed here and there in the drops of chyle small islets of nearly perfectly transparent fat: I am unable to say whether these masses of fat were produced by the aggregation and cooling of the globules of oily matter. The chyle has hitherto been made very little the subject of microscopic examination. It would be especially desirable to know in what relation the globules of the chyle stand to the red particles of the blood; whether the latter bodies are formed from the globules of the chyle, or whether the smaller bodies observed by Sir E. Home in human blood, and by myself in the blood of frogs and birds, are identical with the globules of the chyle. The form of the chyle globules in animals, of which the red particles of the blood are large and elliptical, should be ascertained; which could be done only in the larger reptiles, where the thoracic duct can be more easily found, or in fishes. Rudolphi mentions, that Leuret and Lassaigne have observed that the globules of the chyle in birds are round, although the particles of the blood are oval; but the French observers here spoke not of chyle globules, but of the particles of chyme taken from the intestinal canal.

The source of the red colour of the chyle has likewise been very fully investigated by Tiedemann and Gmelin. They found the red colour of the chyle generally more marked in horses than in dogs, and even more so in the latter animals than in sheep. In dogs it was more distinct when the food had consisted of liquid albumen, butter, milk, bones, meat, or bread and milk. The chyle was white, and the red colour of the coagulum very slight, when the food had consisted of fibrin, gelatin, soft cheese, starch, and butter, or gluten. And neither chyle nor clot were at all red, if the dog had eaten coagulated albumen; nor are they so, according to my own observation, after a meal of bread, milk, and butter. The chyle was likewise devoid of the red tint in dogs killed while fasting, or after they had taken food consisting of starch, milk, raw or boiled beef, beef and wheaten bread, or liquid albumen and spelt-bread; and in cats which had been fed with bread and milk, or boiled beef.

The fluid in the thoracic duct in horses killed while fasting, was of a darker red colour than in horses which had had a feed of oats. The chyle of sheep to which only a little hay or straw had been given, was white with a tinge of red; that of sheep fed with oats, was quite white. From the last-mentioned facts, the experimenters inferred that the chyle contains less red colouring matter, the more nourishing the food which the animal has taken; and that the red colouring matter of the blood was not generated immediately by the digestive process; the red fluid conveyed into the chyle by the absorbents of the spleen more especially must, they observe, give a less marked tinge to the chyle when the matter absorbed from the intestines is more abundant.

In a horse fed with oats, the chyle in the lacteals which had not passed through the mesenteric glands, was white; did not become red on exposure to the air, and yielded a white clot. The chyle taken from the lacteals of the mesentery after they had passed through the mesenteric glands, and that of the thoracic duct, were of a light red colour; the lymph from absorbent vessels of the large intestine was pale yellow, and yielded a white coagulum; that of the absorbents of the pelvis was red, and its clot was of a darker red than that of the chyle of the thoracic duct. From these facts, which agree with the results of Emmert's experiments, Tiedemann and Gmelin draw the conclusion that the red colour of the chyle is imparted to it by the mesenteric glands, and by the lymph of other absorbent glands, and of the spleen, being derived from the blood circulating in the capillaries of these several parts: they remark that the circumstance of its being changed to green by the action of hydro-sulphuric acid, demonstrates that it is identical with the red colouring matter of the blood.

Hewson* first observed that the lymph of the spleen resembles diluted red wine in colour, and contains red globules. Tiedemann and Gmelin observed the red colour, as well when the animals had had food, as when they had been fasting before death. Fohmann† has seen the lymph of the spleen red in rays opened during life, and maintains that the colour is more distinct during digestion, and likewise after long fasting, when it is also perceptible in the lymph of the liver. Rudolphi, on the other hand, says that the lymphatics of the spleen are usually as white as those of the liver and other organs, and that those of other organs also sometimes contain a bloody fluid. I must, however, remark that the contents of no other absorbents than those of the intestinal canal are ever white; and that in some few instances, in which I examined the lymph of the spleen in oxen just slaughtered, I found it in some of the large lymphatics of the colour of dilute red wine. Seiler observed a red tinge in a few instances in some of

* Op. Posth. Ed. Lugd. Batav. 1785.—Experimental Inquiries. London, 1772.

† Saugadersyst. der Fische, p. 45.

the lymphatics running on the spleen in horses; but in most cases it was absent; and in oxen (?), asses, sheep, swine and dogs, the lymph of the spleen was never coloured. The observations of Tiedemann and Gmelin prove distinctly that the red colour of the chyle and lymph is owing to the presence of some of the cruorin of the blood: but it is not yet known whether this red colouring matter is in solution, or attached to the peculiar globules of the chyle and lymph. Hewson, it is true, saw red bodies in the lymph of the spleen; and Emmert states that he saw red globules in the water in which he agitated the red coagulum of chyle, and the serum of chyle still contains globules which might account for Tiedemann and Gmelin having frequently seen it, as well as the coagulum of a red tint. Schultz* and Gurlt† state, that they have found in the chyle, in addition to the proper globules of that fluid, here and there a blood corpuscule; and hence infer that the reddish colour of the chyle is due to the presence of such red particles, of which they suppose the formation to begin in the chyle.

Fibrin of the chyle,—its source.—The firmness of the coagulum of the chyle is different in different animals. The proportion of the moist and dried coagulum in the horse, dog and sheep, is stated as follows by Tiedemann and Gmelin. In 100 parts of chyle:

	of fresh coagulum	of dry coagulum
Of the horse, there were . .	from 1·06 to 5·65 . .	from 0·19 to 1·75
Of the dog	1·36 to 5·75 . .	0·17 to 0·56
Of the sheep	2·56 to 4·75 . .	0·24 to 0·82

The contents of the thoracic duct coagulated more perfectly when the animals were killed while fasting, than when they had taken a meal a short time previously; and the amount of fresh and dry coagulum was greater in the former case. The dry coagulum of the chyle of horses killed while fasting amounted to from 1·00 to 1·75; of horses which had lately taken food, from 0·19 to 0·78 per cent.

Tiedemann and Gmelin have moreover confirmed Emmert's observation, that the proportion of fibrin in the chyle increases with the progress of this fluid towards the thoracic duct. In a horse which recently had a feed of oats, the chyle of the lacteals which had not passed through the mesenteric glands did not coagulate; while 100 parts of the chyle of the lacteals which had passed through those glands afforded 0·37 of dry coagulum, the same quantity of the chyle of the thoracic duct 0·19, and the same quantity of the lymph of the pelvis 0·13.

On the above facts Tiedemann and Gmelin ground their opinion that the fibrin of the chyle is not derived immediately from the food, but is formed in the blood and poured into the chyle and lymph by the

* Syst. d. Circulation.

† Physiol. d. Haussäugethiere.

glands of the absorbent system, and by the spleen. And since the chyle of the lacteals that had passed through the mesenteric glands contained more fibrin than the lymph of the absorbents of the pelvis, they conclude that more fibrin is added to the chyle by the mesenteric glands than by the glands with which the lymphatics of the pelvis communicate. However, the opinion that fibrin is thus added to the chyle is as difficult to prove as the opposite hypothesis, that the albumen of the chyle itself is converted into fibrin. (See page 283.)

To determine the correctness of either, it would be necessary to ascertain by a great number of experiments the quantity of solid ingredients, and particularly of albumen, in the serum of the fluid contained in different parts of the absorbent system. If, for example, it was found that the serum of the chyle of the thoracic duct after the separation of the fibrin contained less albumen than the serum of the lymph of the extremities, and of the chyle of the lacteals, it would be certain that albumen is converted into fibrin in the absorbent system, since it would appear that the albumen diminished in quantity while the quantity of the fibrin increased. The results obtained by Gmelin and Tiedemann, relative to the proportion of solid contents in the serum, were, however, only contradictory. The amount of the solid substances dissolved in the serum varied from 2·4 to 8·7 per cent. In the horse which had been fed with oats,

The serum of the	chyle of the	lacteals contained of solid ingredients	4·9	per cent.
,,	,,	thoracic duct . . .	3·04	
,,	,,	lymph of the pelvic lymphatics	3·1	

In the horse which was killed while fasting, on the contrary,

The serum of the contents of the thoracic duct contained of solid ingredients		4·7	per cent.
,,	,, lymph of lumbar plexus of lymphatics .	3·7	

In whatever the change in the chyle consists,—whether in the addition of new matter, or in the conversion of one of its ingredients into another substance,—it must evidently be effected by the coats of the lacteal and lymphatic vessels, both those which are distinct, and those convoluted or interlaced lymphatics of which the absorbent glands* are formed.

The coats of the absorbents being traversed by capillary blood-vessels, it is possible that the fibrin as well as the colouring matter of the blood may permeate the membranous coats of the vessels and enter the chyle: on account of the greater surface afforded in the mesenteric glands by the convoluted and reticulated vessels of which they are formed, this would take place to a greater extent in them than in other

* See page 270.

parts of the lacteal system. But the red particles themselves cannot in this way enter the chyle from the blood.*

The *analysis of the serum of the chyle* by Gmelin showed that the same salts exist in it as are met with in the intestinal canal. The following are the solid ingredients of the serum of the chyle of the horse, according to that chemist:

Albumen	55·25
Osmazome, with acetate of soda, and chloride of sodium (the most abundant saline ingredient), crystallised in octohedrons, probably from containing some animal matter	16·02
A matter soluble in water and insoluble in alcohol, and resembling salivary extractive matter, with carbonate and a very small quantity of phosphate of soda	2·76
Brown fatty matter	15·47
Yellow fatty matter	6·35
Carbonate and some phosphate of lime obtained by calcination of the albumen	2·76
	98 61

Tiedemann and Gmelin found no traces of the substances used as food in an unaltered state in the chyle; they observed merely that, when the animal had taken butter, the chyle contained an abundance of fatty matter, and in the chyle of one dog which had taken starch they detected sugar.

Comparison of the chyle and lymph.—Both chyle and lymph contain globules; but those of the transparent lymph are very few in number, while those of the chyle are so numerous as to give it a milky appearance. They both contain fibrin, which likewise, however, seems to be contained in smaller quantity in the lymph; for Tiedemann and Gmelin found that 100 parts of the chyle of the lacteals which had traversed the mesenteric glands in a horse previously fed with oats, yielded 0·37 of dry coagulum; while the same quantity of lymph from the pelvis afforded only 0·13. This great apparent difference may, however, be owing to a portion of the numerous globules of the chyle being included with the fibrin in the coagulum. The fatty matter which is not perceived in the lymph, but is contained in so large quantity in the chyle, giving rise to the cream-like pellicle which forms on its surface, constitutes another point of difference. The saline matters appear to be about the same in both.

Comparison of the chyle with the blood. — The chyle, as it is obtained from the thoracic duct, differs from the blood,—

1. In its globules being insoluble in water, while the red particles of

* On the very doubtful hypothesis, that the chyle is poured directly into minute veins in the mesenteric glands, as well as concerning the supposed connection of the veins and absorbents, see page 272.

the blood, with the exception of their nucleus, are readily soluble in that fluid.

2. In its wanting the red colouring matter: (this difference is not constant.)

3. In the form and size of its globules.

4. Its alkalinity, which was noticed by Emmert, Vauquelin, and Brande, is, according to Tiedemann and Gmelin, less marked than that of the blood, and is sometimes absent.

5. The proportion of solid ingredients is less in the chyle than in the blood. One thousand parts of chyle contain, according to Vauquelin, only from 50 to 90 parts of solid matter; while Prevost and Dumas state that 1000 parts of blood contain 216, Lecanu says 185, parts of solid ingredients.

6. In 1000 parts of serum of the blood there are, according to Reuss and Emmert, 225; in 1000 parts of serum of chyle only 50 parts of solid matter. From the serum of the chyle of sheep, dogs, and horses, Tiedemann and Gmelin obtained from 2·4 to 8·7 per cent. of solid matter; while Prevost and Dumas state the amount of solid ingredients in the serum of the blood of those animals to be from 7·4 to 9·9 per cent.

7. The proportion of fibrin is much less in the chyle. Tiedemann and Gmelin obtained from the chyle of the animals just named only from 0·17 to 1·75 per cent. of dry fibrin; and, according to Reuss and Emmert,* 1000 parts of blood of the horse contain 75 parts of (moist?) fibrin, while 1000 parts of chyle contain only 10 parts.

8. The fibrin of the chyle appears to differ somewhat from that of the blood; for Brande has observed that acetic acid dissolves but a small part of the chylous coagulum, which in this resembles albumen, while fibrin of the blood is generally readily soluble in that acid.

9. Chyle contains a large quantity of fat in a free state; the fat of the blood is wholly in a state of combination with other matters: the coagulum of chyle likewise contains fat in a combined state.

10. The chyle, like the blood, contains iron, which it derives from the food, and conveys into the blood; but the metal appears to be in a much less intimate state of combination in the chyle than in the blood, for it can be extracted from it by means of nitric acid, and then forms a black precipitate with tincture of galls, a blue with prussiate of potash. Even the serum of chyle afforded evidence of containing iron when it had been freed from its albumen.† Emmert, however, imagines that the iron contained in the alimentary matters in the small intestine is more highly oxidised than in the chyle, since the fluid of the small intestine of the horse is acid, and since the fluid from a horse's intestine which was filled with digested aliment, after being filtered, afforded, immediately that the admixture was made, a black precipitate with

* Scherer's Journal, v. 164.

† Reil's Archiv. viii. p. 167.

tincture of gall, and a blue one with prussiate of potash; while in chyle the change of colour in each case takes place very slowly.

Death is ordinarily the inevitable *consequence of ligature of the thoracic duct*, ensuing, according to Duvernoy, in fifteen, according to Sir A. Cooper, in from nine to ten days; and in horses, as appears from Dupuytren's experiments, in five or six days. Sometimes the animals do not die, and in these cases we must suppose that there existed several vessels connecting the lower with the upper portion of the thoracic duct; or that there were branches connecting the thoracic duct with the vena azygos, a structure which Panizza has seen in the hog, and Wutzer and I have once observed in the human subject; or we must admit that there were two thoracic ducts, as in birds and tortoises.*

CHAPTER VII.

OF THE FUNCTION OF THE SPLEEN, THE SUPRA-RENAL CAPSULES, THE THYROID, AND THE THYMUS GLANDS.

These are glands unprovided with an efferent duct; they agree in having the common function of impressing some change on the blood which circulates through them, or in yielding a lymph which plays a special part in the process of chylification and sanguification; for the venous blood and the lymph are the only matters returned by them into the general system.

a. OF THE SPLEEN.

Structure of the spleen.†—The spleen is met with only in the vertebrate classes, and in them is nearly constant. Rathke and Meckel have stated that it is absent in the cyclostomatous fishes (the petromyzon and ammocætes). There is a glandular organ near the cardia of the petromyzon marinus, which Mayer‡ regards as a spleen. In the myxine Retzius has found the spleen to be really wanting; an observation which I can confirm, and which I find to apply likewise to the allied genus bdellostoma. With these exceptions, the spleen is universally present in the vertebrata. In the cetacea the organ is divided into several small masses.

In man and mammalia the spleen lies in the fold of peritoneum

* The principal treatises on the chyle are those of Werner, de modo quo Chymus in Chylum mutatur,—Tübingæ, 1800; Horkel's Archiv. für die thierische Chemie, t. i. Heft ii.; Emmert und Reuss, Scherer's Journal, v. p. 154—691; Emmert, Reil's Archiv. viii. p. 145; Marcet, Medico-chirurg. Transact. 1815, vi. 618; Brande, Philos. Transact. 1812; Prout, Annals of Philos. xiii. p. 12. 263; Ant. Müller, Diss. exp. circa Chylum,—Heidelb. 1819; Tiedemann and Gmelin, Rech. sur la Digestion, part ii.

† See Müller, in the Archiv. für Anat. und Physiol. 1834, i.

‡ Froriep's Notizen, 737.

which is continuous with the serous covering of the anterior and posterior surfaces of the stomach, and extends between the great curvature of the stomach, the diaphragm, and the transverse colon; and which, at the part where it connects the stomach to the transverse colon, is called great omentum. This portion of peritoneum passed originally from the spinal column in the middle line to the great curvature of the stomach, forming a mesogastrium,* in which the spleen was developed. The spleen, therefore, is not an organ proper to the left side of the body, of which the fellow of the opposite side is wanting: it should be regarded as an organ originally situated in the middle line, just like the liver, which at first, when its two lobes were equal, did not belong to the right side more than to the left.

The spleen is invested by a strong, fibrous membrane, which sends numerous band-like processes into its interior, so as to support the soft, pulpy, red tissue of the organ. In the red substance there are in many animals contained whitish, round corpuscules, visible by the naked eye, which were first discovered by Malpighi, and of which the existence in the human spleen has been at one time admitted, at another denied.

The corpuscules of the human spleen are described by Dupuytren and Assolant as greyish bodies, devoid of internal cavity, and measuring $\frac{1}{5}$ of a line to 1 Paris line in diameter, and so soft as to take a liquid form when raised on the knife. Meckel describes them as roundish, whitish bodies, $\frac{1}{6}$ of a line to 1 line in diameter, most probably hollow, at all events very soft, and very vascular. Such soft bodies are certainly met with sometimes in the dog and in the cat, and in very rare instances in the human subject. They are the parts which Home, Heusinger, and Meckel describe to swell considerably in animals after drink is taken; an assertion the correctness of which I doubt. I can throw no light on the nature of these bodies; they are very different from the grape-like corpuscules discovered by Malpighi in the spleen of some herbivorous quadrupeds; the following account of which is the result of my own research.

I have found them in the hog, sheep, and ox. They are most easily examined in the hog. Rudolphi's assertion that they do not exist in that animal must have arisen from an error of memory. They are round, white bodies, measuring from $\frac{1}{3}$ to $\frac{1}{2}$ a millimeter [$\frac{1}{7}$ to $\frac{1}{4}$ of a line] in diameter, of equal size, and distinctly circumscribed outline. Their firmness is sufficient to enable them to resist considerable pressure. They neither appear fluid when removed from the substance of the organ, nor collapse, as Rudolphi† incorrectly stated. In the ox they are a little larger than in the hog and sheep. They are seen on the cut surface of the organ, or still better on a torn surface, or after maceration for a short time, when the pulpy substance of the spleen becomes very soft and blackish; while the white corpuscules remain for a much longer time

* See page 497.

† Grundriss der Physiologie, Bd. ii. Abtheil. ii. p. 175.

uncoloured, namely, of a whitish grey, and undissolved. In torn and half-macerated fragments of the spleen of the sheep or hog, the connexion of the corpuscules in bunches may likewise be very well made out, which is done with much greater difficulty in portions of fresh spleen. Heusinger * speaks of it being possible to demonstrate grape-like bunches of the white corpuscules by merely rubbing a piece of the spleen between the fingers, and the statement is correct; but it is true only of the white bodies in the spleen of the hog, sheep, and ox.

On an accurate examination of the corpuscules in the spleen of the hog, I found that none are isolated; that each sends out processes towards one or both sides; and that sometimes, though rarely, they are united in a line like the knots of a cord, each knot sending out other smaller threads: generally they are attached by short pedicles to fibres which are branches of other fibres, or, which is most frequent, they are sessile, and attached by a more or less broad base to the side of ramifying fibres. The fibres which connect them together become smaller in the direction of their ramification, and are evidently branches of larger trunks. The larger threads to which the corpuscules are attached can, by the aid of the microscope, be seen to have a cavity in their interior, and, when traced to their origin, are found to be branches of the splenic blood-vessels.

By means of fine injections I ascertained that the vessels to which they are attached are branches of the splenic artery, and that they are connected more especially with the sheaths with which the arteries of the spleen are provided. They appear to be growths or processes of the sheath, but I will not say that in respect to texture they are identical with it. The most minute branches of the artery are in a certain degree unconnected with the corpuscules, inasmuch as they are distributed chiefly to the pulpy substance of the organ. When the splenic artery has been finely injected, its smaller branches are seen to pass superficially through the walls of the corpuscules rather than to be distributed in its substance.

In the interior of the corpuscules there is a fluid, white, pulpy matter, which consists for the most part of irregularly globular particles, nearly all of equal size, and of about the same diameter as the red particles of the blood, though not flattened like them. Under the microscope they have the same appearance as the granules of the pulpy substance of the spleen, and are of the same size.

The red pulpy substance consists of a mass of red-brown granules, as large as the red particles of the blood, but differing from them in form, being irregularly globular, not flattened. These granules are easily separable from each other. In the mass which they form the minute arteries ramify in tufts, and terminate in the plexus of venous canals

* Ueber den Bau und die Verrichtung der Milz. Thionville, 1817.

into which all the blood of the spleen is poured before it is carried out of the organ by the splenic vein. The anastomosing venous radicles, which are of considerable size, appear to have scarcely any distinct coats. If a portion of the pulpy substance of the spleen is examined more closely, it is seen to be everywhere perforated with small foramina, which are spaces bounded by the reticulated substance of the organ. These spaces are venous canals; on inflating them the organ acquires a cellular appearance, and if they are injected with wax the substance of the spleen will present a great resemblance to the corpora cavernosa penis. There are no true cells in the spleen. The white corpuscules are embedded in the pulpy substance, and not contained in cells, as Malpighi supposed. A fibrous trabecular tissue intersects in all directions the very soft pulpy red substance, and affords support to the texture of the organ.

In the human spleen the Malpighian corpuscules are distinguished with great difficulty. I have recently seen them in a spleen which had been macerated; they are very firm, and much smaller than the greyish soft points sometimes seen in cut surfaces of the spleen, which have been described under the name of the Malpighian corpuscules, but are really very different from them.

Function of the spleen.—We are quite ignorant of the office of the spleen; we merely know that its importance in the economy is not great: the experiments of numerous observers have shown that it may be extirpated without any remarkable ill consequence. Dupuytren observed increased voracity in dogs after the operation; Mayer* states that the lymphatic glands become enlarged, but this is certainly not a constant effect. It has by others been said that the secretion of urine becomes more abundant, but Tiedemann and Gmelin† deny that such is always the case. Mead and Mayer had noticed signs of imperfect digestion after the removal of the spleen; and some writers have stated that the bile becomes very bitter and dark-coloured, both of which the Heidelburg professors likewise deny to be constant phenomena. The refutation of the hypotheses proposed to explain the use of the spleen will not occupy us long; for they either rest on wholly incorrect premises, or they are such as can neither be proved nor disproved.

All the theories which regard the spleen as essentially connected in its function with the liver, can be shown to be fallacious. Doellinger supposes the spleen to be formed merely for the sake of symmetry, to be the fellow of the liver,—the rudimentary liver, as it were, of the left side. But the liver is originally symmetrical; and the spleen is, as we have already described, developed in the middle line. No greater value can

* Med. Chirurg. Zeit. 1815, 3 Bd. 189.

† Versuche über die Wege, &c. p. 105.—Recherches sur l'Absorption, translated by Heller.

be accorded to the circumstance that splenic veins join the vena portæ, and to the hypothesis, thence deduced, that the spleen prepares the blood for the secretion of the bile; for in this respect it does not differ from all the chylopoetic viscera, nor even from the inferior extremities in the lower vertebrata, and the generative organs and air-bladder of fishes.*

Some physiologists imagine, without any reason, that the spleen may exert a de-oxidising effect on the blood; others again believe that it favours the secretion of the gastric juice, because it receives less blood (?) at the time that the stomach is full; while others, as Lieutaud and Moreschi, regard it as a reservoir of blood for the stomach, supposing that the stomach when distended with food may attract more blood to itself, or may press on the splenic artery so as to diminish the quantity of blood sent at that time to the spleen. Dobson's hypothesis† is very similar; he stated that he has found the spleen to have its maximum volume at the time when the process of chymification is at an end,—namely, five hours after food is taken; and to be small and contain little blood seven hours later, no food having been taken in the interval: he hence inferred that the spleen is the receptacle for the increased quantity of blood which the system acquires from the food, and which cannot, without danger, be admitted into the blood vessels generally, and that it regains its previous dimensions after the volume of the circulating fluid has been reduced by secretion. The premises of this theory do not appear to me to be sufficiently proved. Dobson repeated Magendie's experiment of injecting fluids into the veins of an animal, and, he says, with the same result with regard to the spleen, namely, the increase of its size.

The assertion of Defermon,‡ that, when certain substances are taken into the system, the spleen undergoes changes in volume,—that it becomes smaller under the influence of strychnine, camphor, and muriate of morphia,—appears to me likewise to require confirmation. Sir E. Home, resting on the statement that the spleen increases in size after fluids are taken into the stomach, imagined that the fluids found their way by some unknown canals from the stomach to the spleen, and thence to the kidneys; but he afterwards renounced this idea.§ The function of the spleen probably consists in the production of some change, of which the nature is unknown, in the blood which circulates through its tissue, and in thus contributing to the process of sanguification; or in the secretion of a lymph of peculiar nature, which, being mixed with the contents of the lymphatic and lacteal system coming from other parts, tends to per-

* See page 169.

† London Med. Phys. Journal, Oct. 1820.—Froriep's Not. 615.

‡ Nouv. Biblioth. Méd. Mars, 1824.—Froriep's Not. 148.

§ Phil. Transact. 1811.

fect the formation of the chyle. There are no other ways than the lymphatics and veins by which any animal matter, modified by the action of the spleen, can be conveyed away from it. Tiedemann believes that the lymphatics perform this office ; but whether he is correct or not is quite uncertain, and the nature of the change which the animal matter is supposed to undergo is still less known.

The blood of the splenic vein, according to Tiedemann and Gmelin,* does not differ from other venous blood ; they saw it coagulate like the blood of other organs. The older physiologists, and more recently Autenrieth,† maintain, however, that the blood has peculiar characters. Schultz,‡ too, found the blood of the vena portæ of a darker blacker tint than other venous blood, and the dark colour was most evident in animals which were fasting. Neither neutral salts nor the action of the air had the effect of rendering it of a brighter red colour ; its coagulum was less firm than that of other blood, and it contained less fibrin and albumen, but more fatty matter.

Mr. Hewson§ supposed that it was the office of the spleen, as well as of the lymphatic glands and thymus body, to secrete from arterial blood a fluid which, mixed with lymph, should give rise to red blood particles. This, however, cannot be true, for the red particles are formed equally well after the extirpation of the spleen. The reddish colour of the lymph of the spleen, observed by Hewson, Tiedemann, and Fohmann, is not constant.||

Mayer has asserted that the spleen is reproduced after extirpation. He says, that after the lapse of some years he has found in ruminating animals, in the place of the spleen, a body of the size of a lymphatic gland: this would be an interesting fact if it could be satisfactorily proved ; but that is scarcely possible, for animals often have small accessory spleens (splenculi), and in the operation of extirpation a small portion of the organ might be left behind in the body. The presence or absence of the bunches of white corpuscules, above described,¶ might aid in determining whether any substance be spleen or not.

b. Of the supra-renal capsules.

*Their structure.***—The supra-renal capsules are met with in man, in mammalia, in birds, and in a rudimentary state in reptiles, and the

* Rech. sur l'Absorption.—Versuche über die Wege, &c. p. 70.

† Physiologie, ii. 77. ‡ Rust's Magazin. 1835. 325.

§ Experimental Inquiries. || See page 562.

¶ The treatise of Giesker, Anatomisch-physiol. Untersuch. über die Milz,—Zurich, 1835, contains a full account of the opinions of all previous writers, and also some original observations on the structure of the spleen in man, more particularly with reference to the corpuscules.

** From original researches.

sharks and rays. Retzius has described them in the serpents, and the sharks and rays; and Nagel* has found traces of them in crocodiles, in chelonian reptiles, and in serpents. Nagel agrees with Retzius in regarding the fat-body of the frog as a distinct structure from the supra-renal capsule, of which he believes the true analogue to be a line of yellow granular substance on the anterior surface of the kidneys.

The supra-renal capsules are formed of a yellow cortical substance which consists of vertical fibres, and of a dark spongy medullary portion. The only cavity in the interior of the organ is that of the vein which lies in its centre. In the cortical substance the minute arteries and veins are of uniform size, and nearly as delicate as the ordinary capillaries of other parts, and are regularly arranged in a radiated manner, running parallel to each other from the surface towards the interior. They may be shown either by injection of the artery or vein, and are seen to anastomose so as to form very long meshes. On the external surface of the organ there is a capillary network of the ordinary form. All the straight venous branches of the cortical substance pour their blood into the spongy venous tissue of which the medullary substance, for the most part, consists, and from which veins arise that form the large vena supra-renalis in the interior of the organ. By forcing air into the vein the whole medullary tissue may be distended. The structure here described may be very easily demonstrated by fine injection, and is the same in the ox, calf, sheep, and hog, as in man; the organs in the different animals being distinguished merely by external form and aspect.† To determine whether the blood of the organ in its passage through the vascular tissue of the cortical substance undergoes any peculiar change, it would be necessary to tie the vena supra-renalis in the living animal, which on the left side is practicable, and then to examine the fluid in the interior of the vein and in the inner substance of the organ. There are no grounds for the belief that the supra-renal capsules are more frequently deficient than other organs in the acephalous monsters.

The function of the supra-renal capsules is unknown. The researches of Meckel and myself have shown that in the human embryo they are originally larger than the kidneys; and in an embryo one inch in length, for example, even conceal the kidneys from view. It is not until the tenth or twelfth week that the latter organs equal the supra-renal capsules in size. In other mammiferous animals I have never found the supra-renal capsules of larger size than the kidneys at any period. They have no physiological connection with the urinary organs. In a case in which the left kidney was anormally situated on the right side, I found the corresponding supra-renal capsule in its usual place; while in another

* Müller's Archiv. 1836.

† See Nagel, loc. cit.

instance, where the kidney was atrophied, the corresponding organ in question was of its natural size and structure.

c. Of the Thyroid body.

Structure.—The thyroid body, or gland, appears to contain very small cells, the connection of which, as well as the proper structure of the organ, are unknown. In goitre the cells become enlarged, and contain an albuminous matter. *Function* unknown.

d. Of the Thymus gland.

*Structure.**—The thymus gland, in proportion to the size of the body, is largest in the fœtus, but continues to grow after birth, and remains of considerable size during the first year, after which it gradually diminishes until it has about the time of puberty wholly disappeared.

In the calf the organ consists of lobes which are divisible into smaller lobules. Each lobule is constituted of numerous secreting cells, and larger cavities or reservoirs.

In the human subject the largest lobuli do not exceed a pea in size. On more accurate examination, says Sir A. Cooper, the lobuli being drawn out and separated from each other are found to be connected in two spiral chains which resemble necklaces of large and small beads. To examine their internal structure, a thin superficial lamina must be cut from one of the lobules or from several at once; a number of small cavities are then seen, in which the abundant white fluid of the gland is in part contained. From these cavities the fluid is transmitted into a general reservoir, which forms a common connecting cavity between the different lobules, and is lined by a delicate membrane. On the inner surface of the reservoir little openings are seen leading into pouch-like dilatations, by which the cavities of the lobules communicate with the common receptacle. The openings into the reservoir are not, however, so numerous as the lobules, more than one lobule being connected with each pouch. The essential point in the structure, therefore, is that the small cells or cavities in the substance of the lobules communicate with a pouch-like cavity at the base of each lobule, which again lead by a small opening into the common reservoir. Sir A. Cooper describes a large lymphatic, which is easily injected, to be connected with each cornu of the thymus in the fœtal calf, and to terminate at the point of junction of the two jugular veins with the superior vena cava. But the connection of the lymphatics with the cavities in the gland has not been demonstrated.

The fluid of the thymus is whitish, contains microscopic white particles, and is coagulable by alcohol, mineral acids, and heat. Liquor potassæ converts it into a tenacious substance; one hundred parts con-

* After Sir A. Cooper. The Anatomy of the Thymus Gland. London, 1832.

tain sixteen parts of solid matter. The saline ingredients are muriate and phosphate of potash and soda, with a trace of phosphoric acid. The nature of its proximate animal components is imperfectly known. Fibrin appears not to be one of its ingredients, and this circumstance distinguishes it from lymph and chyle.

Function of the thymus.—The anatomical facts detailed by Sir A. Cooper would seem to indicate that a peculiar albuminous fluid is conveyed from the thymus gland to the veins by the lymphatics. It appears quite vain to attempt by hypothesis to explain how the organ can contribute to the formation of the blood in the fœtus and child. Every hypothesis which regards it as an organ adapted to the necessities of fœtal life, and not to those of the child, must be incorrect.*

CHAPTER VIII.

OF THE ELIMINATION OF THE EFFETE DECOMPOSED MATTERS.

Life is attended with a constant decomposition of organic matter; the causes of this we have already investigated.† We have seen that the action of external stimuli is necessary for the continued manifestation of life. Their action produces a change in the composition of the organic matter of the body; and, while more important organic compounds are generated, the useless ingredients of the substances which suffered decomposition are excreted. But even the conversion of the new nutriment into blood is necessarily attended with the excretion of useless elements. The apparatus by which these effete matters are eliminated, not formed, are the skin and kidneys. The nature of the excretions is the subject of our present consideration. The organic conditions on which secretion and excretion generally depend have been treated of in the section on secretion.

Relative quantity of the excretions.—Dr. Dalton ‡ has made a number of experiments in his own person to determine the proportion which exists between the quantity of the aliment and that of the excretions in a healthy subject. In the first series, instituted in the month of March, and continued during fourteen days, 91 ounces, or nearly 6 pounds, was the mean quantity of solid and fluid aliment taken into the system daily. The average amount of urine excreted each day was $48\frac{1}{2}$ ounces, of fæces 5 ounces, making together $53\frac{1}{2}$ ounces; so that, provided the weight of the body remained the same, the amount of matter exhaled daily by the skin and lungs must have been $37\frac{1}{2}$ ounces. The second series of experiments was instituted in summer, in the month of June; the daily amount of solid excreta was then less by 4 ounces;

* Mr. Tyson, in the London Medical and Surgical Journal, January 1833, put forward the hypothesis that the office of the thymus is to receive during fœtal life the blood which afterwards is sent to the lungs.

† Pages 35 and 364.

‡ Edinb. New. Philosoph. Journ. 1832, 1833.

while the quantity of the urine was greater by 3 ounces, the quantity of matter carried off by exhalation was $44\frac{1}{2}$ ounces,—6 ounces more, consequently, than in the spring. In autumn half the daily amount of food was got rid of by exhalation. Dr. Dalton calculated that the aliment which he took in twenty-four hours contained about $11\frac{1}{2}$ ounces of carbon. Now he estimates the proportion of carbon in the urine at $1\frac{1}{4}$ per cent.; it would, therefore, in $48\frac{1}{2}$ ounces amount to $\frac{5}{10}$ or $\frac{6}{10}$ of an ounce. A hundred parts of fæces contain 75 parts water, and of the remainder not more than 10 parts are carbon. In 5 ounces of fæces consequently there would be but half an ounce of carbon, and $10\frac{1}{2}$ ounces of this element must be got rid of by cutaneous and pulmonary transpiration. By earlier experiments* Dr. Dalton had ascertained that the amount of carbon exhaled from his lungs in twenty-four hours averaged about $10\frac{1}{4}$ ounces. The average quantity of water expired was at most $20\frac{1}{2}$ ounces. So that in twenty-four hours $30\frac{3}{4}$ ounces of effete matters—water and carbon—are excreted from the lungs, leaving $6\frac{3}{4}$ ounces to be exhaled by the skin, of which $6\frac{1}{2}$ ounces would be water and a quarter ounce carbon. According to this calculation, then, the quantity of the matters exhaled by the lungs is five times greater than that of the cutaneous transpiration. Dr. Dalton estimates that of the six pounds of new matter taken daily as nutriment, one pound consists of carbon and nitrogen, the rest being for the most part water.

Excretion of foreign matters.—Foreign matters, which have been taken up into the circulation, are not excreted at the same time and with equal facility by all the free surfaces of the body. On the contrary, it is observed that one or other of the excreting organs manifests a greater attraction for certain foreign substances, and excretes them more readily than others. Thus it has been shown by Magendie† and Tiedemann‡ that alcohol and camphor are exhaled by the lungs; while saline and many colouring matters pass off, either changed, or in their original state, more especially by the kidneys. It may be stated generally that those matters which are prone to pass out of the system by a certain secreting organ, are likely to be stimulants of that organ, and hence we may explain the stimulant action of the neutral salts on the kidneys, these salts being generally excreted in an unchanged state with the urine. The results of Woehler's researches§ on the excretion of foreign matters by the kidneys will be detailed in the article on the urine.||

1. *Cutaneous exhalation and perspiration.*

The skin is the seat of a two fold secretion,—a fatty matter, and a

* Manchester Memoirs. New Series. Vol. ii. p. 27.

† Bulletin de la Société Philom. 1811.

‡ Zeitschrift für Physiol. S. 2.

§ Ibid. Bd. i.

|| Page 589.

vapour. The first is formed by the sebaceous follicles of the skin; its properties and composition have not hitherto been examined. In the fœtus it forms an unctuous coating to the skin, and consists then, according to Frommherz and Gugert, of an intimate mixture of a fat similar to cholesterine, and albumen; the latter, however, may be derived from the liquor amnii.

The sources of the watery exhalation are the skin and the lungs. During strong exercise and exposure to great external warmth in some diseases, and also when evaporation is prevented by the application of oiled silk or plaster, the perspiration collects on the skin in the form of drops of fluid—the sweat. The sweat is secreted by the minute spiral follicles or sudoriferous canals, discovered by Purkinje and Breschet, which are distributed over the whole surface of the skin.*

Quantity of the cutaneous transpiration.—Since the laborious researches of Sanctorius, who instituted ingenious experiments to ascertain by weighing the quantity of the matters lost by exhalation, more exact investigations have been carried on with the same view by others, especially by Lavoisier and Seguin.† The result of their inquiries was that during a state of rest the average loss by cutaneous and pulmonary exhalation in a minute is from seventeen to eighteen grains,—the minimum eleven grains, the maximum thirty-two grains. To ascertain the amount of the cutaneous and pulmonary transpiration individually, Seguin enclosed his body in a bag or dress of silk covered with elastic gum, open at the top, and provided with a copper mouth-piece. The bag, or dress, being closed by a strong band above, and the mouth-piece adjusted and gummed to the skin around the mouth, he was weighed, and then remained quiet for several hours, after which he was again weighed. The difference in the two weights indicated the amount of loss by pulmonary exhalation. Having taken off the air-tight dress, he was immediately weighed again, and a fourth time after a certain interval. The difference between the two weights last ascertained gave the amount of the cutaneous and pulmonary exhalation together; by extracting from this the loss by pulmonary exhalation alone while he was in the air-tight dress, he ascertained the amount of cutaneous transpiration. The repetition of these experiments during a long period with great care afforded the following results:

1. However much the quantity of the food may vary, the weight of the body, if not subjected to exertion, returns in twenty-four hours to about the same standard; so that,

2. If under otherwise similar circumstances the quantity of the food varies, or if, the quantity of the food remaining the same, the loss by exhalation is different, the solid and fluid excretions are proportionably increased or diminished.

* See page 439. † Mém. de l'Acad. des Sc. 1790. Ann. de Chim. t. 90.

3. When digestion is imperfect, exhalation is less active.

4. Digestion being good, the quantity of the food has no great influence on the amount of exhalation.

5. The exhalation is least abundant immediately after food is taken.

6. But the greatest loss of weight from exhalation takes place during digestion.

7. The maximum loss by exhalation, cutaneous and pulmonary, in twenty-four hours, is 5 lb.; the minimum, 1 lb. 11 oz. 4 dr.

8. The cutaneous transpiration is influenced both by the state of the atmosphere and by the state of the body itself.

9. The mean loss by exhalation in a minute is 18 grains, of which 11 grains pass off by the skin, 7 by the lungs.

Dryness of the atmosphere has the effect of increasing the exhalation from the skin and lungs, although the greater exhalation has a cooling influence; while a great elevation of the external temperature is attended with a contrary result.* The cutaneous exhalation is more rapid when the surrounding air is in motion, and when the atmospheric pressure is not great. M. Edwards makes a distinction between the exhalation which is the result of mere physical evaporation, and which would take place in dead bodies under the same circumstances, and that which depends on a vital function; and he calculates that when the temperature of the atmosphere is not above 68° F., the vital transpiration contributes only $\frac{1}{6}$ to the total sum of cutaneous exhalation. The product of the physical evaporation is nearly pure water, that of the organic transpiration contains animal matters: the former is suppressed when the air is saturated with moisture, the latter when the body is exposed to cold. The pulmonary exhalation is, according to M. Edwards, solely the effect of evaporation, which undergoes diminution in an air saturated with moisture, though it be of the same or of a higher temperature than the body. The different states of external temperature affect so much the function of transpiration, that we must extract the most important results of Edwards's researches on the subject. The temperature being the same, water is a better conductor of caloric than watery vapour, and vapour than dry air; and hence the latter, cæteris paribus, is supported by the animal body longer without inconvenience. Moist and warm air is more heating, because it communicates its caloric more readily to the body, and because the physical evaporation is not so free in it as in dry air. A warm atmosphere saturated with water in a gaseous form, particularly if in the form of vapour, excites a more active transpiration than dry air of the same or even of a higher temperature. If its temperature is lower than that of the body, dry air conducts away less heat, and hence is less cooling than moist air, which is a better conductor of caloric.

* Edwards, Influence des Agens Physiques sur la Vie. Dr. Hodgkin's translation, p. 168 to 180.

The components of the cutaneous exhalation are in part matters capable of assuming the form of vapour, such as carbonic acid and water, and in part other matters which are deposited on the skin and become mixed with the sebaceous secretion. Thenard collected the cutaneous perspiration in a flannel shirt which had been previously washed in distilled water, and found it to consist of chloride of sodium, acetic acid, some phosphate of soda, traces of phosphate of lime, and oxide of iron, together with an animal substance. In sweat which had run from the forehead in drops, Berzelius* found lactic acid, a matter soluble in alcohol (osmazome), a small quantity of a substance insoluble in alcohol, a considerable quantity of chloride of sodium, and muriate of ammonia. The fluid exhaled from the skin has been more recently examined by Anselmino. He placed his arm in a glass cylinder, and closed the opening around with oiled silk, taking care that the arm touched the glass at no point. The cutaneous exhalation collected on the interior of the glass, and ran down as a fluid: on analysing this, he found in it acetate of ammonia and carbonic acid. The exhalation of carbonic acid by the skin had been previously observed by Abernethy and Mackenzie; while Priestley, Fourcroy, and Gordon failed to detect it in their experiments.† Collard de Martigny‡ detected in the cutaneous exhalation both carbonic acid and nitrogen in very variable proportions; they were not constantly present, but were exhaled in great abundance after muscular exertion, and after meals. Sometimes the nitrogen was exhaled alone, as happened in the experiments of Ingenhouss, Trousset, and Barruel. Sometimes the gas was almost wholly carbonic acid, as had been observed by Milly, Cruikshank, Jurine, Abernethy, and Mackenzie. M. Collard states that the nitrogen was more abundant after the diet had consisted principally of animal substances, carbonic acid when food of a vegetable nature had been taken. M. Collard has collected the gas evolved from the skin by placing over it a glass funnel, closed by a stopper above, and filled with distilled water, and hence infers that the carbonic acid is exhaled in the gaseous form, since it is evolved without the contact of atmospheric air.

Anselmino§ has given the following analysis of the fluid sweat: in 100 parts of the dried residue there were,

Matters insoluble in water and alcohol (chiefly calcareous salts)	2
Animal matter soluble in water, insoluble in alcohol (regarded by Anselmino, in the opinion of Berzelius without sufficient reason, as salivary matter), and salts of sulphuric acid	21
Matters soluble in dilute alcohol (chloride of sodium and osmazome)	48
Matters soluble in pure alcohol (osmazome, lactic acid, and its salts,—regarded by Anselmino as acetic acid and acetates)	29
	100

* Chimie Animale, p. 324.

† Meckel's Archiv. iii. p. 608.

‡ Magendie's Journal, x. 162.

§ Tiedemann's Zeitschrift, iii p. 321.

Berzelius mentions sal ammoniac and lactate of ammonia also as ingredients of the perspiration.

In the ash of the dried residue of the sweat, Anselmino found carbonate, sulphate, and phosphate of soda, and some potash, with chloride of sodium, phosphate and carbonate of lime, and traces of oxide of iron.

In the sweat of the horse, which is known to deposit a white powder, Fourcroy found urea, but Anselmino could not detect it.

Several parts of the body afford a perspiration with peculiar properties, due perhaps to the secretion of the sebaceous follicles. Thus the perspiration of the axillæ is ammoniacal, and that of the genital organs contains butyric acid. Several animals, again, and many men, have a perspiration of peculiar odour: in animals, however, this odour frequently arises from the products of special glands,—of the anal glands, for example.

The *object of the cutaneous exhalation* is not elucidated by its analysis, for the matters met with in it are also constituents of the urine. Since, however, as Seguin's experiments show, its quantity bears so close a relation to that of the food and to that of the other excretions, we can in some measure understand how its sudden suppression, by disturbing the normal composition of the circulating fluids and their distribution in the body, may give rise to great disorder of the animal economy. The agency of the transpiration in preserving the body under the influence of high temperatures has been already explained.*

The cutaneous exhalation and sweat are true secretions; they are not the result of the mere evaporation of those ingredients of the blood which are capable of taking the form of vapour. This is proved by the fact that in some diseases the perspiration is quite arrested, although the temperature of the skin is elevated; such, for example, is the case in many febrile diseases in which the influence of the nerves on the skin is in a state of depression. Moreover, an especial relation exists between the cutaneous exhalation and the urinary secretion; it would appear, indeed, that the skin has the office of separating from the blood those matters more particularly which, at the temperature of the body, take a gaseous form, while the kidneys remove from it the more liquid excreta. But there is another relation, that of alternation of action between the skin and kidneys. When the urine is secreted in excessive quantity, as in diabetes, the skin is dry. In hot seasons and in warm climates the urinary secretion is less abundant, the cutaneous secretion more so; in winter the reverse is the case; and in diseases the same alternation of action is observed. But the cutaneous secretion is modified not only by its antagonism with other secretions,† but also by many other causes, of which some have their seat in the skin itself, others are dependent on the sympathy between it and other organs. With regard to the first kind

* See page 79. † See page 473.

of these causes, it may be remarked, that gentle stimulants applied to the skin itself,—for example, hot baths,—or acting on it through the medium of the blood,—as diaphoretics,—increase its secretion; but that if the irritation of the skin is raised to too great a degree, it becomes red and hot, and its perspiration ceases, and the secretion of the skin, like that of most other parts, is wholly arrested by inflammation. Hence extensive inflammations of the skin, by arresting its secretion, and thus disturbing the balance in the distribution of the circulating fluids, have a tendency to excite antagonistic actions of a morbid nature, such as inflammations of the mucous membranes. Extensive burns have been observed to be followed by inflammation of the mucous membrane of the intestines or lungs; and in the exanthematous diseases, in which a morbid matter is excreted by the skin, the danger of the supervention of internal inflammation becomes more imminent, not merely in proportion to the suppression of the process by which the morbid matter is eliminated from the blood, but also in proportion to the violence of the inflammation by which the function of the skin is arrested.

The action of the skin is very much modified likewise in accordance with the states of the nervous and vascular systems.

In febrile affections the secretion of the skin and mucous membranes diminishes in proportion as the influence of the nervous system in these parts is depressed. In other states that are not febrile, on the contrary, a sudden withdrawal of nervous energy, such as takes place in syncope and during the sway of depressing passions, gives rise to a profuse cold sweat. The conditions on which these great changes in the cutaneous secretion under certain circumstances depend, have not at present been submitted to a satisfactory physiological investigation.

2. *The secretion of urine.*

The urinary secretion is the means of carrying out of the system decomposed and effete animal matters, such as urea and uric acid,—the essential components of the urine,—superfluous saline matters, and, either in an altered state or in their original condition, foreign matters which have accidentally entered the circulation.

The urine is an excretion met with through a great extent of the animal scale. Even insects secrete uric acid by the biliary or rather Malpighian vessels.* Uric acid has indeed been found in entire insects; thus Robiquet† detected it in cantharides, and it has hence been inferred that this acid is distributed generally throughout their body. But, in analysing the entire body of an insect, the contents of the above-named vessels are necessarily included. There is a secretion of urine in the mollusca likewise. Jacobson has detected uric acid in the secretion of the saccus calcareus (l'organe de la viscosité, Cuvier), the efferent

* See page 519.

† Annal. de Chimie, 76.

duct of which, running by the side of the rectum, terminates close to the anus.*

The urine.†—The urine of the human subject is transparent, amber-coloured, and of an aromatic odour; has a bitter taste, and a strong acid reaction. The urine of oxen, horses, rabbits, and several other herbivorous animals, is alkaline; in some it is acid in the perfectly fresh state only. The urine of herbivorous mammalia is more turbid and often viscous, and undergoes decomposition less rapidly than the urine of carnivora. The specific gravity of human urine varies between 1·005 and 1·030; in some diseases, particularly in diabetes, it is sometimes as high as 1·050. The urine occasionally becomes turbid in cooling, and deposits in such cases a grey or pale red sediment, which is redissolved when the fluid is heated. After exposure to the air for a few days, the urine acquires an ammoniacal odour and an alkaline reaction; and a white, slimy pellicle, in which, as well as on the inner surface of the vessel, small white crystals of phosphate of ammonia and magnesia show themselves, forms on the surface.‡

a. Essential constituents of the urine.—Besides the mucus of the urinary passages, which is rarely visible in the excretion, Berzelius enumerates the following as essential ingredients:

Water	933·00
Urea	30·10
Free lactic acid, lactate of ammonia, osmazome soluble in alcohol, and extractive soluble in water	17·14
Uric acid	1·00
Mucus of the bladder	0·32
Sulphate of potash	3·71
Sulphate of soda	3·16
Phosphate of soda	2·94
Biphosphate of ammonia	1·65
Chloride of sodium	4·45
Muriate of ammonia	1·50
Phosphate of lime and magnesia	1·00
Silica	0 03
	1000·00

1. *Urea.*—This substance was discovered in the urine by Cruikshank. It is procured by evaporating urine carefully to the consistence of honey, acting on the inspissated mass with four parts of alcohol, then evaporating the alcoholic solution, and purifying the residue by repeated solution in water or alcohol, and finally allowing it to crystallise.§ The urea appears in the form of delicate silvery acicular crystals; long, narrow, four-sided prisms; or, in the impure state, scales. It is colourless when

* Meckel's Archiv. vi. 370.

† After Berzelius, Woehler and Liebig.

‡ Berzelius, Chimie Animale, p. 342.

§ For an account of other methods of procuring it, consult Gmelin's Chemie, iv. 1014, and Berzelius, loc. cit. p. 370.

pure; when impure, yellow or brown: is without smell, and of a cooling, nitre-like taste; has neither an acid nor alkaline reaction, and deliquesces in a moist and warm atmosphere. At 59° Fahr. urea requires for its solution less than its weight of water, and is dissolved in all proportions by boiling water; it requires five times its weight of cold alcohol for its solution; it is not precipitated by tannin. At 248° Fahr. it melts without undergoing decomposition; at a still higher temperature ebullition takes place, and carbonate of ammonia sublimes; the melting mass gradually acquires a pulpy consistence, and, if the heat is carefully regulated, leaves a grey-white powder, cyanic acid, which is likewise formed and sublimes when uric acid is submitted to dry distillation. Urea forms compounds with both acids and bases without neutralising them. It is remarkable that the presence of urea causes sal ammoniac to crystallise from its solutions in octohedrons, in place of cubes; and muriate of soda to crystallise in cubes, in place of octohedrons. Nitric acid combines with urea, and precipitates it from its concentrated watery solution. Urea contains more nitrogen than any other animal product. Dr. Prout found it to be constituted of

Nitrogen	46·65
Carbon	19·97
Hydrogen	6·65
Oxygen	26·65

Woehler has discovered that urea may be formed artificially.*

We owe to Prevost and Dumas the knowledge of the important fact, that, after both kidneys have been extirpated, urea can be detected in the blood; whence may be inferred, that the reason of this substance not being found in the blood in the healthy state, is, that it is excreted from it as soon as formed.† Their discovery has been confirmed by Vauquelin and Legalas,‡ by Mitscherlich, and by Tiedemann and Gmelin.§

The source of the urea, from what organ it enters the circulation, is unknown. It can at present merely be asked, by way of conjecture, whether perhaps the urea may not be generated in the lungs during the chemical process which the blood undergoes in respiration, and by which higher organic compounds are formed. It may, however, be produced in other parts also during the conversion of the new nutrient materials into the proper components of the organic fluids. The important question, whether the urea is formed from the decomposition of that animal matter only which has already been organised, or whether it is derived from the nutriment newly introduced into the blood, being in the latter case a useless product of digestion, has been discussed at page 152. To determine it, it would be necessary to keep animals without food, then

* See page 3, in note. † See page 151. ‡ Ibid.

§ Tiedemann's Zeitschrift, v. 1. See also Nysten, Recherches de Chimie et de Physiol. Pathol. Paris, 1811, p. 263. Meckel's Archiv. ii. 678.

extirpate the kidneys, and examine the blood to see if it contained urea.

In several diseases the urine contains no urea; for instance, in hysterical attacks, in which the secretion becomes very watery. The organic matters are then wanting; the urine contains only the saline ingredients. In diabetes mellitus, the urine contains, in place of urea, sugar (the sugar of grapes,) and the urea reappears in proportion as the quantity of the sugar diminishes. Here, then, an ordinary constituent of the urine, which contains so large a proportion of nitrogen, is replaced by a substance into the composition of which nitrogen does not enter at all. The sugar of the urine is, according to Dr. Prout, constituted of

Carbon	39·99
Hydrogen	6·66
Oxygen	53·33

In diabetes insipidus, in which the urine contains no saccharine matter, the place of the urea is supplied by another substance, which is in great part soluble in alcohol, and agrees in its characters with osmazome. In anasarca, deficiency of urea in the urine is supplied in equal proportion by the presence of albumen, and the urine is then coagulable by heat. This albuminous state of the urine is more especially frequent in dropsy attending the degeneration of the kidneys, pointed out by Dr. Bright. On the other hand, Marchand * has several times found urea in the fluid of dropsical swellings. The presence of albumen in the urine, with deficiency of urea, has likewise been observed in cases of chronic inflammation of the liver with constant dyspepsia,† as well as towards the termination of all diseases producing emaciation.

2. *Uric or lithic acid.*—We obtain uric acid from the sediment of human urine, or from the urine of birds and serpents, by dissolving the evaporated urine in warm water, filtering the solution, and precipitating by means of muriatic acid. Uric acid crystallises in the form of delicate white,—when impure yellow or brownish, scales; it is devoid of taste and smell, and reddens moistened litmus paper; requires, according to Prout, more than 10,000 times its weight of cold water for its solution, but somewhat less boiling water. It is insoluble in alcohol and ether. By dry distillation it is decomposed; carbonate of ammonia being first sublimed, afterwards hydrocyanic acid in large quantity, a brown empyreumatic oil, and, lastly, a crystalline substance, cyanic acid, according to Woehler,‡ with which a quantity of urea is mixed. The elementary composition of uric acid has been stated by Dr. Prout to be—

* Müller's Archiv. 1837, p. 440.

† Rose and Henry, in Meckel's Archiv. ii. 642.

‡ Poggendorf's Annal xv. 529.—Berzelius's Chimie Anim. p. 348.

Nitrogen, in his first analysis	40 25	In a later analysis	31·12
Carbon	34·25		39·87
Hydrogen	2·75		2·22
Oxygen	22·75		26·77

Urine, while warm, holds in solution much more uric acid than an equal quantity of boiling water will dissolve, and this has induced Dr. Prout to think that the uric acid in the urine is in the state of urate of ammonia. The uric acid which is precipitated during the cooling of the urine is, however, in the free state. Duvernoy* contends that the uric acid is held in solution in warm urine by means of the colouring matter. The precipitate of uric acid is at first powdery and grey, but assumes by degrees a rose-red colour, and crystallises as it dries. The red or brick-dust tint of uric acid is due to a colouring matter which is combined with it: in intermittent fevers this red colour is unusually deep. Berzelius regards it as still very doubtful whether, or not, the red colour of the precipitate in the urine in fevers is dependent on the presence of purpurate of ammonia.

Duvernoy detected no essential difference between the deep-coloured red urine and the urine of the crisis of fever, which deposits a sediment. Both have a stronger acid reaction, and a redder colour, and contain a larger quantity of uric acid than natural. The critical urine merely had a larger proportion of uric acid, and deposited it more readily.

Liebig and Woehler† have discovered that uric acid contains urea in a peculiar state of combination; that at all events urea, with several other products, can be procured from uric acid. Uric acid brought to the consistence of a thin pulp with water, was heated nearly to the boiling point, and then superoxide of lead was added, which gave rise to the developement of carbonic acid gas. The fluid which filtered from the mixture yielded, on cooling, colourless or yellowish brilliant hard crystals of allantoic acid, the substance found in the fluid of the allantois of ruminants. The supernatant liquid being poured off, evaporated, and again cooled, crystals of urea formed in it. The superoxide of lead was converted into a white mass, consisting of oxalate of lead. The products of this decomposition, then, are allantoic acid, or rather, since it is not an acid, allantoin, urea, oxalic acid, and carbonic acid. Allantoin is composed of:

Carbon	30·66	or 4 atoms
Nitrogen	35·50	4
Hydrogen	3·75	6
Oxygen	30·08	3

It may therefore be regarded as a compound of four atoms of cyanogen, with three atoms of water. Its elements require three atoms of water

* Untersuchungen über den Menschl. Urin. Stuttg. 1835. 8.

† Poggendorf's Annal. p. 41. 561; and the British Annals of Medicine for Sept. 16, 1837.

to give it the composition of oxalate of ammonia, into which it is converted by the action of alkalies and sulphuric acid. If now we admit, with Liebig and Woehler, that the urea pre-existed in the uric acid, by subtracting from

	Carbon.	Nitrogen.	Hydrogen.	Oxygen.
1 atom uric acid . . .	10	8	8	6
1 atom urea . . .	2	4	8	2
we shall have as remainder . .	8	4	0	4

which are the elements of four atoms of cyanogen, and four atoms of carbonic oxide. These chemists therefore regard uric acid as a compound of urea with a substance composed of cyanogen and carbonic oxide, which in the above process is converted by the action of the superoxide of lead into oxalic acid and allantoin.

The urine of many animals differs from that of the human subject in the proportions of the urea and uric acid in them. The urine of carnivorous mammalia contains both urea and uric acid. Vauquelin and Boindet * have denied that it contains any uric acid, but Hieronymi † obtained some of this acid from urine of the feline tribe. In 100 parts of urine he found 13·220 parts of urea, with osmazome, and free lactic acid, and 0·022 parts of uric acid. The urine of herbivorous animals contains urea, but no uric acid; the place of which, in the urine of graminivorous animals is supplied by hippuric acid, forming hippurates. The urine of birds contains abundance of superurate of ammonia; that of carnivorous birds is said by Coindet to contain urea, which does not exist in the urine of birds which feed on vegetable substances, although the superurate of ammonia exists in the latter also. Uric constitutes $\frac{1}{60}$ of the weight of the urine of the ostrich. The consistent pulpy urinary secretion of birds owes its white colour to the presence of urate of ammonia. The urine of serpents and lizards also is white, and that of serpents becomes quite solid and hard soon after it is excreted; it contains urates of potash, soda, and ammonia, and some phosphate of lime, but not a trace of urea, which, according to Schultz,‡ is wanting in the urine of lizards likewise: the urine of the amphibia and chelonia, on the other hand, is quite different; that of frogs and toads is very watery, and is stated by Dr. J. Davy to contain chloride of sodium, uric acid, and a little phosphate of lime. Professor Magnus and I have examined a considerable quantity of the yellowish-brown urine which was contained in the bladder of a large example of the testudo nigra, brought alive from the islands of Gallopagos by Meyen, and found in it not a trace of uric acid, but 0·1 per cent. of urea, and a brown colouring matter soluble in water and alcohol, in potash and in muriatic acid. It appears, then, that the presence or absence of urea and uric acid (of which the former contains

* Froriep's Notiz. No. 272.

† Jahrb. der Chem. u Phys. 1829, iii. 322.

‡ Froriep's Notiz. xiii. 119.

46, the latter 40 per cent. of nitrogen) stands in no constant relation to the nature of the food of the animal. The only fact bearing on the point is, that in herbivorous mammalia the uric acid is replaced by hippuric acid, which contains only 7 per cent. of nitrogen. It is stated likewise by Chevreul, that when dogs are kept for a long period on vegetable food, their urine becomes like that of herbivora, ceasing to contain any uric acid or phosphate of lime.*

Of all diseases, it is in gout especially that the proportion of uric acid in the urine, which is more acid and deposits more sediment, is greater; although during the febrile state which accompanies the paroxysms, as in other cases of fever, the urine is deficient in that acid.† The abundance of uric acid in gouty habits, however, is likewise shown by the concretions which form in the joints, and which consist of urate of soda, with some urate of lime. It is not improbable that the perspiration likewise of patients labouring under gouty and calcareous diseases contains uric acid.

All the foregoing circumstances render it very probable that the source of the uric acid lies much deeper than the point of its excretion, and that its production is intimately connected with the nature of the food, and with the process of sanguification, since its proportion in the urine diminishes when the food consists of vegetable substances only.

In diabetes mellitus, in which the place of the urea in the urine is supplied by saccharine matter, uric acid is still present,‡ and, according to M. Wittstock, hippuric acid also.

3. *Hippuric acid* is met with in the urine of young children (?), and of graminivorous animals, in the state of hippurate of soda. It is procured by evaporating the urine, and precipitating by muriatic acid; it forms long, transparent, four-sided prisms, is without taste, or is but slightly bitter, and reddens moistened litmus paper. Gmelin has classed it as a modification of benzoic acid among the substances which contain no nitrogen; but Liebig regards it as a peculiar acid, and not as a mere compound of benzoic acid with animal matter; and, since it gives out ammonia when decomposed, it must contain azote. It is difficult of solution in cold water, more soluble in boiling water; alcohol dissolves it in greater proportion, ether in less. Its composition, according to Liebig, is,

Carbon	63·032
Hydrogen	5·000
Nitrogen	7·337
Oxygen	24·631

* Huenefeld, Physiol. Chemie, i. 150.
† Berzelius, Chimie Anim. p. 404. See also Nysten, loc. cit.
‡ Woehler, Berzelius's Jahresb. vi. 283.

4. *Lactic acid* is, according to Berzelius, a general product of the spontaneous decomposition of animal matters within the body; it is generated in large quantity in the muscles, is saturated by the blood and its alkali, and is carried out of the system in the acid urine of man and animals; it is the principal cause of the acidity of the urine, although this secretion contains likewise superphosphates of ammonia and lime.

5. *Salts of the urine.*—The secretion of the human kidney contains both sulphates and phosphates. Berzelius supposes that the acids in these salts are the product of the chemical action of the kidneys, because in the other fluids of the body there are merely traces of sulphates, and but a small quantity of phosphates, while the urine abounds with both; but his reasons do not justify the conclusion which he draws. Berzelius imagines that the sulphur which enters into the composition of the fibrin, albumen, &c. is converted in the kidneys into sulphuric acid, while the other elements unite to form ammonia, urea, &c. He holds the same opinion with regard to the phosphorus which exists in several of the solids of the body. In the urine of herbivorous animals the place of the phosphates is supplied by salts of carbonic acid. The experiments of Berzelius and Woehler prove that the urine does not constantly hold carbonic acid gas in solution. The silicic acid seems to be derived from the water taken as drink. The bases of the salts of the urine are potash, soda, ammonia, lime, and magnesia; the salts are chloride of potassium, muriate of ammonia, phosphate of lime (a supersalt, the phosphate of the bones is a subsalt), and a small quantity of fluate of lime.*

Nysten† has investigated the differences between the urine secreted subsequently to the digestion of food,—" urina chyli,"—and the limpid, tasteless urine secreted after fluids have been taken,—the " urina potûs;" the latter he finds to contain thirteen times less urea than the former, four times less of the sulphates, muriates, and phosphates of soda and ammonia, and sixteen times less uric acid. Urine secreted during the existence of inflammation (peritonitis) contained three times more urea than the urina chyli, more of the soluble salts, and a large quantity of albumen, which is not a constituent of healthy urine. In the cold stage of fever the exhalation from the skin is diminished, and the urine becomes more watery; but this does not arise, Berzelius thinks, from the water which ought to pass off by the skin being now got rid of through

* For a more detailed account of the saline substances in the urine, as well as of its doubtful constituents, and the extractive matter soluble in pure alcohol, see the Chimie Animale of Berzelius. The variations in the proportion of the solid constituents of the urine dependent on the food have been investigated, without reference to their chemical nature, by Chossat. (Magendie's Journal, v. 65—225.) On the subject of the urine and its secretion consult Meckel's Archiv. ii. 629—704, where the observations of different authors are collected; and Dr. Prout's work on Diseases of the Urinary Organs.

† Loc. cit. and Meckel's Archiv. ii. 648.

the kidneys, for the quantity of the urine itself is less at this time. In the hot stage, the colour of the urine becomes darker; and the chloride of silver, which produces no precipitate as long as the urine preserves its acid reaction, now throws down a sediment. As the fever advances, the urine becomes more saturated, and begins to afford a precipitate with alum, and at last with nitric acid, showing an increase in the quantity of albumen which it contains.* As the fever declines, the free acid reappears in the urine, which at the same time deposits a sediment in cooling, and this is usually denominated a crisis by the urine. (Duvernoy, however, has observed, that the urine is acid during the whole course of the fever.) Berzelius remarks, that the sediment of the crisis of fever is nothing more than the ordinary sediment, with a rather larger quantity of the red colouring matter, and sometimes some nitric acid in an unknown state of combination. In fevers of a periodical type the urine in each paroxysm passes through the three states just described.

b. Accidental constituents of the urine.—Woehler† has performed a series of careful experiments relative to the passage of substances from the intestinal canal into the urine. The following are the results which he obtained:

1. Matters which, when taken into the stomach, cannot afterwards be detected in the urine: iron, lead, alcohol, sulphuric ether, camphor, oil of Dippel, musk, and the colouring matters of cochineal, litmus, sap-green, and anchusa root. After fluids impregnated with carbonic acid have been drunk, this gas cannot be detected in any quantity in the urine.

2. Matters which pass off by the kidneys after suffering change or decomposition: ferrocyanuret of potassium or prussiate of the peroxide of iron and potash (blausaures eisenoxyd'kali), converted into a compound of the same elements with a less proportion of cyanogen, or prussiate of the protoxide of iron and potash (blausaures eisenoxydulkali); the compounds of potash and soda with the tartaric, citric, malic and acetic acids changed into carbonates; the hydrosulphuret of potassium for the most part converted into sulphate of potash; sulphur in the state of sulphuric acid, and sulphuretted hydrogen, iodine in the state of a hydriodate, oxalic acid, vinic acid, gallic acid, succinic acid, and benzoic acid in combination with alkalies; hence the inutility of giving acids as remedies for calculous disorders.

3. Matters which pass unchanged into the urine: carbonate, chlorate, nitrate, and sulphocyanate of potash, hydrosulphuret of potassium (which is in greater part decomposed), ferrocyanuret of potassium with the smaller proportion of cyanogen or prussiate of the protoxide of iron and potash, (blausaures eisenoxydulkali,) borax, muriate of baryta, silicate of potash, tartrate of nickel and potash, and many colouring matters,

* Berzelius's Chimie Animale, p. 402.

† Tiedemann's Zeitschrift, i. Band.

such as those of soluble indigo, or sulphate of indigo, gamboge, rhubarb, madder, logwood, red beet, whortleberries, mulberries, cherries; many odoriferous matters also, in part changed, such as oil of turpentine (producing the odour of violets in the urine,) the odorous principles of juniper, valerian, assafœtida, garlic, castor, saffron, opium, the intoxicating principle of the agaricus, muscarius, and, in the state of disease, fatty oil.

All substances excreted with the urine must be in solution, they must not be in the state of granules.*

The matters which do not pass off with the urine are either eliminated from the system in other ways,—for instance, by exhalation from the surface, as is the case with camphor,—or they are reduced to an insoluble condition in the intestinal canal itself. Woehler directs attention to the fact, that the salts which are excreted with the urine generally increase the action of the kidneys. Many other medicines which are called diuretics, such as digitalis, are, he observes, termed so incorrectly; thus the action of digitalis consists in the removal of the cause of dropsy, the fluid being then carried off in the usual way; so that it is not more a diuretic than quinine given for the relief of the dropsies which are produced by intermittent fever.

The office of the kidneys, according to Woehler's researches, does not consist merely in the excretion of urea and uric acid; all soluble and not gasiform matters, which do not suffer decomposition in the system, but more especially the superfluous water, are got rid of by means of them. If the excretion of water by the kidneys is lessened on account of that fluid being deposited in other parts of the body, as in dropsy, the urine acquires a deeper colour, which indicates merely that less water is excreted.

The carbonates of the alkalies taken by the mouth render the urine alkaline, and dissolve the lithic acid; their exhibition is a tolerably certain means of counteracting the lithic acid diathesis; the vegetable acids and their salts with the alkalies, being converted into alkaline carbonates in their passage through the body, they may likewise be used with effect for the same purpose. This plan of treatment is, however, only applicable in cases of gravel, or when the calculi are small; for when there are large stones in the bladder, an alkaline state of the urine renders the earthy phosphates insoluble, and may cause them to be deposited as a new crust around the original calculus.†

The excretion of superfluous water from the blood by the kidneys appears to take place with extreme rapidity, it nearly keeping pace with the absorption of watery fluids from other parts of the body into the blood, which thus maintains its normal composition.

* See the remarks on the hypothesis of the metastatic presence of pus in the blood and urine, at pages 277 and 278.

† Woehler, loc. cit. p. 317.

The time occupied by the transit of different substances from the intestines into the blood, and thence into the urinary secretion, has been discussed at page 238. Westrumb detected prussiate of potash in the urine within a period varying from two to ten minutes from the time of its introduction into the stomach. Stehberger* has instituted experiments with reference to this question in a boy, who had inversio vesicæ. The following are the results:

Name of Substance.	*Time at which first detected in the urine.*	*Time at which it was excreted in greatest quantity.*	*Time at which it ceased to be perceptible.*
Madder after the lapse of	15 min.	1 hour	9 hours.
Indigo	15	$1\frac{1}{4}$	$4\frac{1}{2}$
Rhubarb	20	$1\frac{1}{3}$	$6\frac{1}{3}$
Gallic acid	20	$2\frac{1}{2}$	11
Decoction of logwood	25	$1\frac{1}{4}$	$6\frac{3}{4}$
Colg. principle of whortleberries	30	2	$8\frac{3}{4}$
" " Black cherries	45	$1\frac{1}{4}$	
Astringent principle of uva ursi	45	$1\frac{3}{4}$	$7\frac{1}{3}$
Pulp of cassia fistula	55	4	24
Ferrocyanuret of potassium	60	.	$3\frac{3}{4}$
Inspissated juice of elder	75		

The urine collects in the urinary bladder, the sphincter of which, like that of the anus, is ordinarily in a state of contraction. When the quantity of the urine has increased to a certain degree, the action of the sphincter becomes feeble, and contractions of the fundus of the bladder take place. The expulsion of urine may, however, be opposed at will by means of the musculus pubo-urethralis, (Wilson's muscle,) and perhaps likewise by a voluntarily increased contraction of the sphincter. The voluntary expulsion of the urine is effected by the simultaneous action of the diaphragm and abdominal muscles, which diminishes the capacity of the abdominal cavity. The contractions of the urinary bladder are not always subject to the will; but nevertheless, when the bladder is affected by the gradually increased stimulus of the accumulated urine, we seem to acquire some voluntary influence over it. Erection, and the act of expulsion of the urine, are here excluded from consideration. Paralysis of the lower part of the spinal cord is attended with incontinence of urine.

* Tiedemann's Zeitschrift, ii. 47.

BOOK THE THIRD.

Physiology of the Nerves.

SECTION I.

Of the Properties of the Nerves generally.

CHAPTER I.

OF THE STRUCTURE OF THE NERVES.

*a. Of the principal forms of the nervous system.**

THE first great distinction to be made in the forms of the nervous system in the animal kingdom, is between that of vertebrata, in which the brain is not pierced by the œsophagus, and is continued into a spinal cord; and that of invertebrata, in which the brain is always represented by a nervous ring through which the œsophagus passes. This nervous ring of the invertebrata presents, on the dorsal aspect of the œsophagus, a large ganglion, or brain; while there is likewise another enlargement or ganglion occupying the lower part of the ring, and situated below the œsophagus, from which the rest of the nervous system, whether it consists of single nerves, or of a cord with a series of ganglionic enlargements, as in the annelida, crustacea, insecta, and arachnida, takes its origin.

The relation in which the nervous system of invertebrate animals stands to that of the vertebrata is a problem which has long occupied the minds of anatomists and physiologists. Ackermann, Reil, and Bichat compared the ganglionic system of invertebrata with the sympathetic nerve of the higher animals; and the same proposition has very recently been started anew by Serres and Desmoulins. Scarpa, Blumenbach, Cuvier, Gall, and J. F. Meckel have, however, on better grounds, denied the existence of such an analogy; and the greater number of these anatomists have regarded the abdominal cord of the articulata simply as the analogue of the spinal cord of the vertebrata. Meckel and Ph. v. Walther, supposed that, in the part of the nervous system which in the invertebrata is continued from the brain into the trunk of the body, both the spinal cord and sympathetic system of the higher animals are still united; and that, while it has in all cases the function of the two, it in the mollusca approaches more nearly to the type of the sympathetic,

* See a more extended view, by J. Müller, in the Nova Acta Nat. Cur. t. xiv. and in Meckel's Archiv. 1828.

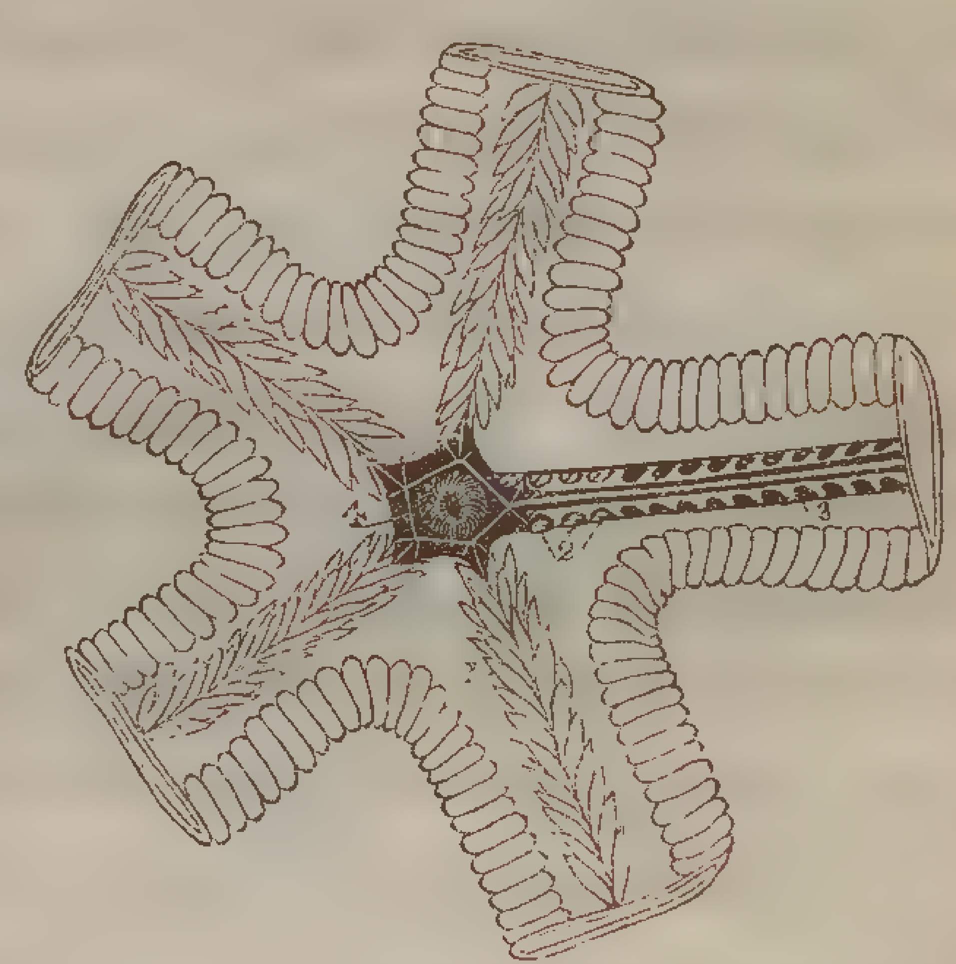
in the articulata to that of the spinal cord. Treviranus and E. H. Weber, lastly, imagined that the ganglia of the abdominal cord of the articulata must be looked upon as nothing more than the ganglia of the spinal nerves, which have coalesced; the intermediate cords being merely the first rudiments of the medulla spinalis. The question has been at length decided by the discovery that in most articulate animals, and in all insects, there is, besides the abdominal cord, a second system of nerves destined solely for the viscera, which consists likewise of a series of delicate ganglia more minute than those of the abdominal cord, attains its greatest developement in the formation of plexuses on the intestinal canal, and particularly on the stomach, and is connected by radicle fibres with the brain.* Traces of a nervous system exist, according to Ehrenberg, even in the infusoria; at all events, he has seen them in the rotifera.

Among the more known forms of the nervous system in the lower animals, the three following types may be distinguished.

1. *Type of the Radiata.*

Similar members arranged around one centre.—The primitive form of the nervous system is the ring, which in the invertebrata generally is known as the œsophageal ring. Its simplest form is met with in the radiata, in which the ring is still without ganglionic enlargements, or a cord-like prolongation. (See fig. 42.) The distribution of its branches corresponds with the radiate division and structure of the animal. There being no prolongation of the body of the creature into an articulated trunk, there is likewise no nervous cord developed as a prolongation of the œsophageal ring. The repetition of similar organs in the periphery of a circle is the character of the type according to which the animal is here formed, and hence all the nerves given off from the œsophageal ring are similar; no one is especially the prolongation of the ring, and no one part of the ring has especially the function of the brain. All the radiating branches of a nervous circle, of which no one has a greater importance than the rest, constitute together what in the higher animals is represented by the principal nervous cord.

Fig. 42.†



* See the account of the organic nervous system of the invertebrata in the 5th chapter of the 2nd section of this Book.

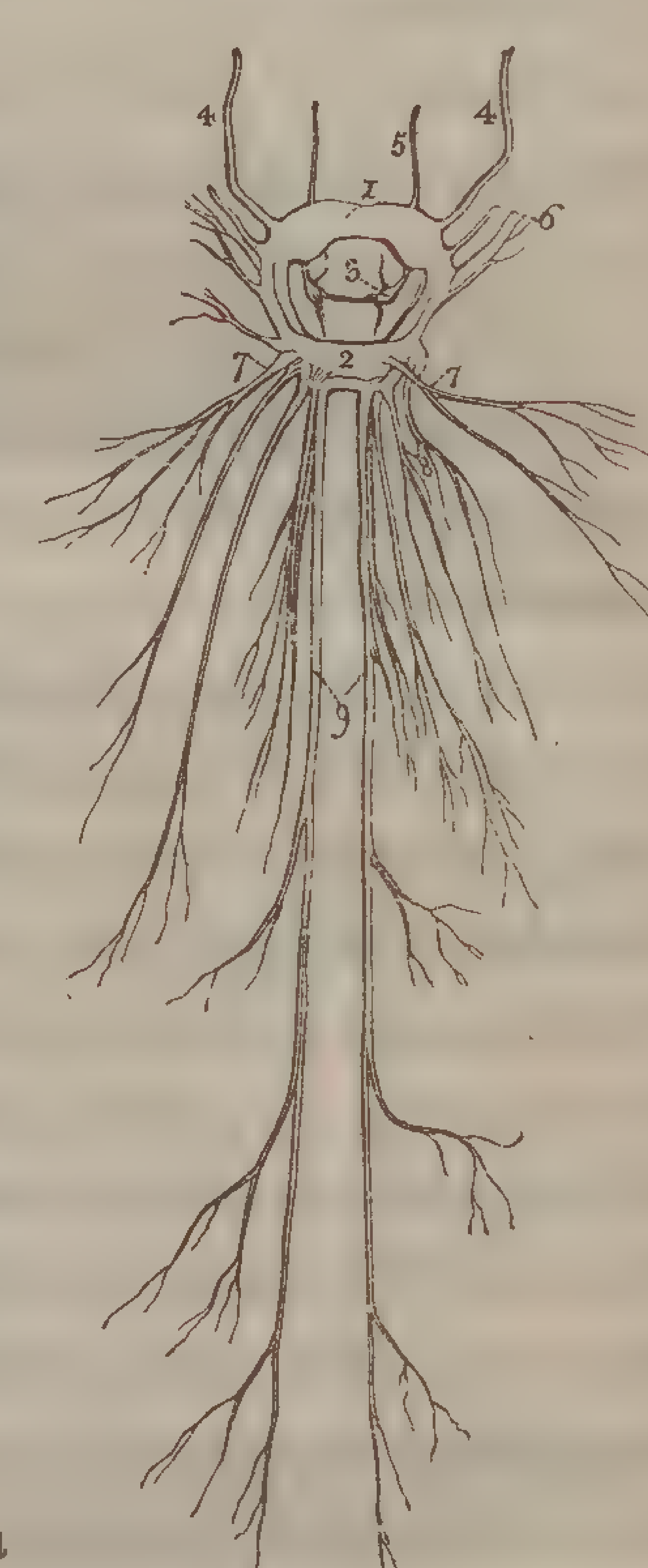
† [Nervous system of the asterias, after Tiedemann.—1. The feet; 2. the feet cut across; 3. the openings through which the feet projected; 4. the nervous ring surrounding the mouth, giving off three branches to each ray.]

2. *Type of the Mollusca.*

No division into members, the viscera enclosed in a common muscular sac. —In molluscous animals the primitive form of the nervous system undergoes changes which only correspond to the modifications that have affected the whole organisation. The symmetry of the radiate type is lost; and, as one most essential character, there is a want of the articulate structure of the other invertebrata. The molluscous animal consists merely of a convoluted mass of viscera in sufficient number to constitute an individual animal system, of which the proper animal or sensitive functions seldom exceed an awkward touch and a sluggish locomotion.

The fundamental œsophageal ring is present here also; but, there being no radiate divisions of the body, the nervous ring does not give off radiating branches. There are nerves of sense, nerves for the viscera, and nerves for the muscles; the viscera not being arranged with any symmetry or order of succession, and there being no regular series of locomotive members, there is not required in the nervous system any succession of similar parts. (See fig. 43.)

Fig. 43.*



The sole developement which the nervous system in this type undergoes, consists in the formation on the œsophageal ring and its nerves of ganglia, from which branches are given off. The grades which this developement is observed to pass through are the following:

1. Ganglia on the œsophageal ring at its superior and inferior parts, (supra-œsophageal and infra-œsophageal ganglia,) as in the gasteropods (see fig. 43); or lateral ganglia on the œsophageal ring, and on the nerves arising from the ganglia of the ring, as in acephala.

2. The œsophageal ring developed into a large cerebral mass, as in cephalopods.

3. *Type of the Articulata.*

The body divided into a series of similar or identical parts, the contents of

*[Nervous system of the common black slug (limax ater).—1. The supra-œsophageal ganglion. 2. The infra-œsophageal ganglion. The lateral cords uniting them are double in this and many other mollusca, as was shown by Berthold (Müller's Archiv. 1835). 3. The small anterior sub-œsophageal ganglia, similar to these described by Cuvier in the limnæus. These are connected each by a long and delicate filament with the supra-œsophageal ganglion, and by a cross filament with each other; they also send branches forwards towards the mouth, and backwards along the œsophagus to the stomach. 4. The optic nerves. 5. Nerves to the upper lip. 6. Nerves to the small tentacles and the muscles about the mouth. 7. The nerves to the pulmonary sac. 8. Nerves to the genital sac, &c. 9. Large nerves of the mantle].

all of which are either similar or identical.—The fundamental character of the articulate animals is, that the body is formed of a succession of rings either similar or identical, which again contain either similar or the same parts of the vascular system and viscera. The organs are no longer included in a convoluted mass by a muscular sac; they are extended for the most part in one direction, namely longitudinally; and the muscular sac has become divided into a number of separate muscles for the different segments of the body. To correspond with this structure, the œsophageal ring and its ganglia are repeated in the form of the gangliated nervous cord. (See fig. 44.)

Fig. 44.*

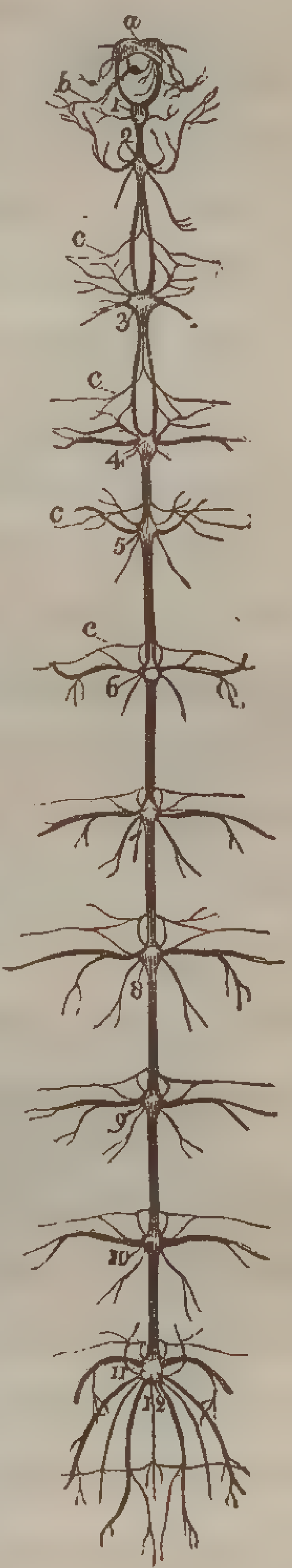
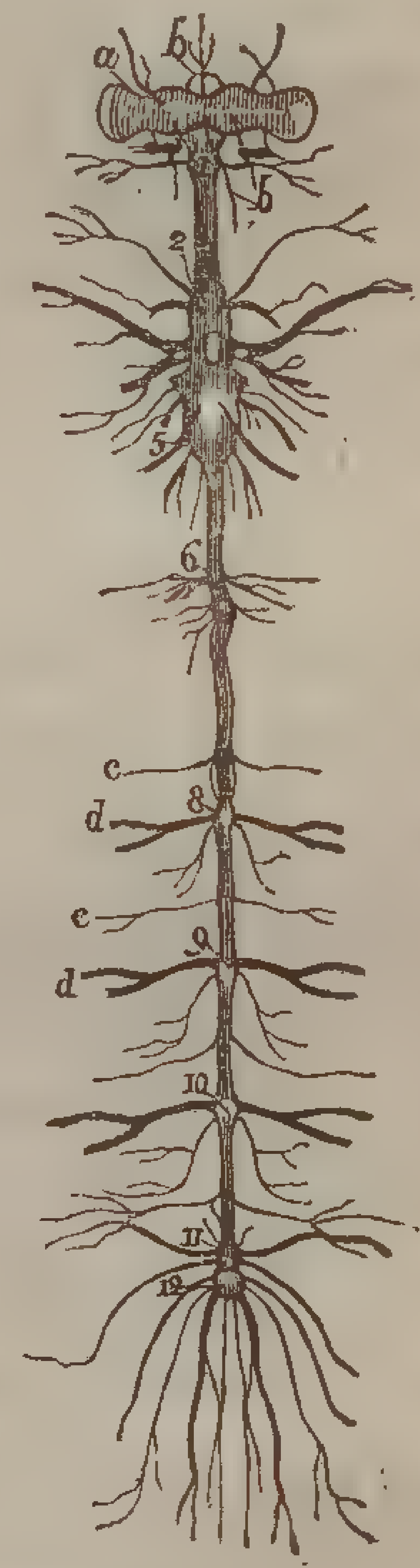


Fig. 45.†



This is the case in annelida, insecta, arachnida, and crustacea. The brain in all the species of these classes seems to be, without exception, superior to the œsophagus.‡ In insects the special nervous system of the viscera becomes distinctly developed.

The union of several of the ganglia of the abdominal cord, the disappearance of some, and the fusion of others into larger masses during the metamorphoses of insects, in accordance with the necessities of the parts which have become more highly developed (see fig. 45), have been already described at page 399. In some few insects all the ganglia and loops of the double abdominal cord are united into one solid column from which all the nerves of the articulated body radiate, but this column is connected with the cerebral ganglion by means of the œsophageal ring, which remains open. This is the structure in the scarabœus nasicornis even in the larva state. Here then

* [The nervous system of the sphynx ligustri in the larva state after Newport.—a. The supra-œsophageal ganglion or brain; 1, 2, 3, to 12, the ganglia of the abdominal cord giving off nerves laterally in each segment. b. The median visceral nerve arising by two roots from the supra-œsophageal ganglion: two nerves arise also from the brain on each side, and form a small ganglion; these likewise belong to the visceral or sympathetic system. c. The interganglionic or transverse nerves.]

† [Nervous system of the sphynx ligustri in the perfect or imago state.—The letters and cyphers refer to the same parts as in the preceding figure: c. are the interganglionic or transverse nerves; d. the nerves given off by the ganglia.]

‡ In the scorpion, as in other articulata, the œsophagus passes through the œsophageal ring; but the posterior or inferior enlargement of the ring is larger than the an-

the gangliated cord is converted into a simple cord, and thus the brain and spinal marrow of vertebrate animals would seem in fact to differ in form but little from the nervous system of invertebrata. There remains as peculiar to the latter animals only the passage of the œsophagus through the nervous ring. On the other hand, we see that in the lower vertebrata the ganglionated structure is again met with in the spinal cord at the points where large nerves arise from it: thus there are several ganglionic enlargements of the cord in the cervical region in the flying fishes (triglæ), and there are enlargements of the spinal cord in chelonia, birds, and mammalia at the points corresponding to the origin of the nerves of the upper and lower extremities.

There are no grounds for comparing the nervous system of molluscous animals to the sympathetic nerves of vertebrata. The absence of the chain of ganglia in the former animals is the consequence of their body not consisting of a series of segments. The union of the ganglia in a series is an accidental circumstance, which has its origin not essentially in the nervous system itself, but in the general structure of the body. Hence, even in the articulate classes, when the division of the body into segments is absent or subordinate, the chain of ganglia is replaced by ganglia situated on the different nerves arising from the brain, as in mollusca; such is the case in the phalangita. The ganglia of the mollusca belong therefore in part to the nerves of the viscera, and are destined for the organic functions; while those cerebral nerves, and their ganglia, which are distributed to the organs of motion, as the mantle (in the sepia), and are capable of exciting voluntary motions, are wholly analogous to the muscular nerves arising from the gangliated cords of the articulata, and are quite distinct from visceral nerves.

b. Of the minute structure of the Nervous substance.

Primitive nervous fibres.—The nerves are constituted of large and small parallel fasciculi, which are invested by a membranous neurilema. These fasciculi, examined along the course of a nervous cord, are found to be connected with each other at intervals; but the parallel primitive fibres contained in these fasciculi run in apposition with each other merely, they do not unite: even where the fasciculi appear to anastomose, there is no union of fibres, but merely an interchange of fibres between the fasciculi.

The primitive fibres of the nerves* are very similar in form and size in different animals; they are in all cases simple threads, are never formed of globules. In the human subject their diameter is, according to Krause,

terior, which circumstance it was which formerly misled me to the belief that here the brain lies below the œsophagus. In the phasmæ also the brain is placed as in all insects, though in 1826 I thought differently.

* See Plate ii. fig. 1.

from $\frac{1}{370}$ to $\frac{1}{184}$ of an English line; according to Prof. R. Wagner, $\frac{1}{277}$: in the frog, the last observer states them to measure $\frac{1}{184}$ of a line in diameter. They vary, however, very much in size, and are frequently, especially the grey fibres, much more minute than the above measurements indicate. The capillary blood-vessels do not ramify on the nervous fibrils, for they exceed these fibrils in size; they merely form a network which lies between the fibres of the nerves. Fontana appears to have been the first who had a correct idea of the structure of the primitive fibres. He distinguished in them an external tubular portion, which, when highly magnified, has a wrinkled aspect, and a solid internal portion, which forms a smooth homogeneous thread. He was able to separate the tubular sheath from its solid contents in some fibres. Thus he says: "The extremities of the nerves were placed in water, and I ran the point of the needle along them to break the cylinders, or deprive them in some way of their irregularities. I succeeded at length in meeting with one that had the form described by fig. 6. About half of this cylinder was formed of a transparent and uniform thread; and the other half was almost twice as thick, less transparent, irregular, and rugged. I then suspected that the primitive nervous fibre was formed of a transparent cylinder, smaller and more uniform, covered with another substance, the nature of which was perhaps cellular. The observations I made afterwards confirmed me invariably in this hypothesis, which at length became an established fact. I have very often seen the two parts that compose the primitive nervous cylinder. The exterior one is unequal and rugged; the other, a cylinder which seems formed of a particular transparent homogeneous membrane that appears to be filled with a gelatinous, consistent humour."*

In the plates which Fontana gives, the primitive nervous cylinders are represented in part still invested by the tube, in part free from it. These observations of Fontana are quite in accordance with those recently made by Remak, who first directed attention to the paragraph in the work of Fontana. Remak describes the contents of the nervous cylinder to be either a perfectly solid fibre of rather less diameter than the cylinder itself, or a flattened pale filet separable by pressure for a considerable extent here and there from the investing tube, which is prone to become wrinkled or puckered. He could not detect any more minute fibrous structure in this filet, although it sometimes became split into several threads.†

The great size of the so-named primitive fibres of the nerves, as compared with the minute elementary parts of muscles, the cellular and other tissues, excites a doubt as to whether the fibre contained in the nervous cylinder is really its most minute element. In fibres of the thickness of the ordinary primitive fibres, which Schwann ex-

* Fontana on Poisons, page 236. † See Müller's Archiv. 1837, p. iv. Jahresb.

amined in the mesentery of the frog, he saw other much finer filaments, which issued from the larger fibre. Treviranus observed in several nervous cylinders streaks running longitudinally, and he even saw distinctly more minute elementary filaments in the so-called primitive cylinders: in the spinal nerve of a crucian (cyprinus carassius,) the minute filaments measured 0.0013 of a millimeter [$\frac{1}{1627}$ of a line], the nervous cylinder 0.0053 of a millim. [$\frac{1}{384}$ of a line] in diameter; in a rabbit the diameter of the minute filaments was 0.0016 millim. [$\frac{1}{1322}$ of a line], that of the including cylinder 0.0099 millim. [$\frac{1}{213}$ of a line].

Fibres of the cerebral substance.—The fibres of the brain were known to Fontana. He describes* them as being cylinders filled with a gelatiniform fluid, but his notion of the intestine-like convolutions of these tubes is quite incorrect. He attributed too much importance to the curved disposition of the fibres, which is an accidental state produced in the preparation of the nervous substance for the microscopic examination; the primitive fibres of the brain and spinal cord have for the most part a tolerably straight direction. Ehrenberg, however, has described the tubular structure of the cerebral fibres, and their arrangement in the brain and spinal cord, very accurately. He states that they run generally in straight lines, and do not anastomose. He saw them divide in but very few instances, as in the spinal cord sometimes. The division of the fibres may, however, be frequent even in the brain, since the mass which the diverging fibres constitute evidently increases between the medulla oblongata and their radiated expansion in the grey matter of the outer part of the optic thalamus. The nature of the contents of the delicate tubes in the brain was not hitherto quite accurately known. It appears to be rather gelatinous than solid; some indeed have found it of oily consistence. Remak states that it is, as in the fibres of nerves, a coherent thread; but, like the tube itself, of a much more delicate nature. The primitive fibres or tubes of the brain and spinal cord, and those of the optic, olfactory, and auditory nervès, have a peculiarity, discovered by Ehrenberg,† which distinguishes them from the primitive fibres of other nerves. On the slightest compression, namely, they assume a beaded appearance, that is, they present a succession of enlargements, between which the cord is narrowed.‡ Fibres and tubes of this kind are called varicose. Ehrenberg found no others than these in the brain and spinal cord, and in the nerves of special sense. The other nerves appeared to him to be composed of the stronger cylindrical fibres which have a more distinct sheath; the sympathetic nerve contained both the cylindrical and varicose fibres. This difference in the character of the fibres promised at first to afford a means of classing the nerves. The tendency of the tubes in some cases to become varicose

* On Poisons, p. 242.

† Poggendorf's Annal. xxviii. Hft. 3.—Abhandl. d. K. Akad. zu Berlin aus d. J. 1834. Berlin, 1836. p. 605.

‡ See plate ii. fig. 2.

certainly shows that they have some peculiarity; but it seems to depend merely on a greater delicacy of the membrane forming them. The primitive fibres of the brain, spinal cord, and nerves of special sense, examined before they are subjected to pressure, appear of uniform diameter, not varicose; and the fibres of other nerves, again, are rendered varicose by compression. The primitive nervous fibres in all parts, in the brain as well as in the nerves, were found by Treviranus to be while fresh for the most part straight, and not varicose.* Volkmann† could not always find varicose fibres in the nerves of special sense. The observations of Lauth and Remak‡ also tended to show that an arrangement of the nerves according to the cylindrical or varicose form of their primitive fibres is scarcely possible, since single varicose fibres are met with more or less frequently in the most different nerves. One and the same fibre sometimes presented the varicose form at intervals, and the fibres of the nerves generally in young animals are prone to exhibit this appearance.

The observations of Treviranus, Valentin, and Weber, would seem to show that the fibres of the brain, spinal marrow, and all nerves, are, in the perfectly fresh and uninjured state, quite uniformly cylindrical, without any enlargements, but that the varicose appearance may be produced by pressure. Notwithstanding the proneness of the fibres of the brain and spinal cord to present the varicose appearance, I have frequently succeeded in separating a lamella of cerebral substance with so little violence that the fibres preserved their uniform cylindrical aspect; and I, like other observers, have seen the fibres of this form in the optic nerve and retina likewise. The fibres seemed to me to suffer most injury when it was attempted to cut too thin laminæ from the soft cerebral substance. The valve of Vieussens affords an excellent opportunity of examining the fibres in a natural thin lamella of cerebral substance, without the interference of the knife. It was in the valve of Vieussens that Weber examined them.

It is, however, a characteristic property of the fibres of the brain, and the nerves of special sense, that they are exceedingly prone to become varicose. No other tissue has this property; and, in enumerating the characters of the cerebral fibres, it cannot be omitted. It is not quite certain on what this property depends.

The structure of the very extensile and elastic spinal cord of the petromyzon is, I have found, very peculiar. It tears with facility into threads; and consists, for the most part, of fibres which are very much flattened, and of which the breadth is equal to that of the primitive fibres of the nerves of the ox. Besides these band-like fibres, there are smaller fibres, and others again still more minute.

* Beiträge zur Aufklärung des organischen Lebens. Bremen, ii.

† Neue Beiträge zur Physiologie des Gesichtsinnes. Leipz. 1836.

‡ Müller's Archiv. 1836. 145.

White and grey fasciculi in the nerves.—It is well known that the fasciculi of nervous fibres in the sympathetic nerves have for the most part a grey aspect, while those of the cerebro-spinal nerves are white. But the latter nerves also contain some few grey fasciculi mingled with the white; and, in many parts of the sympathetic nerve, there are white fibres mingled with the proper grey, or organic fibres. (See Section ii. Chapter 4.) Remak has seen both white and grey fasciculi in portions of the sympathetic taken from various regions; the white fasciculi are probably motor and sensitive fibres derived from the cerebro-spinal nerves, while the grey are destined to rule over the organic functions. The organic nerves owe their grey colour to the fibres composing them, which, according to Remak, differ in structure from the white fibres. The latter are not only much larger than the grey; the difference of the tube and enclosed fibre is in them always distinct, while the more delicate grey fibres have rather a homogeneous aspect. The surface of the grey fibres is here and there beset with very minute granules, similar to those on the twigs of the minute blood-vessels (for instance, in the brain).

The structure of the anterior motor, and that of the posterior sensitive roots of the spinal nerves, have been made the subject of comparative examination by Ehrenberg together with myself, and we detected no difference between them.

Course of the fibres and their arrangement in the nerves. — A knowledge of the course of the primitive fibres in the nerves is of the utmost importance. For, although an exact acquaintance with the ramifications of the nerves is indispensable, yet, in the study of the actions and properties of the nervous system, we must at last come to the question, Where do the primitive fibres contained in a nervous fasciculus arise, and where do they terminate? It is, at least with reference to many questions concerning the functions of the nerves, a matter of indifference into what fasciculus the fibres enter, or how soon they issue from it; since, as will be seen directly, they themselves (the primitive fibres) remain distinct and isolated throughout their course; and this is the first and most important point to be decided. If the primitive fibres never anastomose, it will follow that the cerebral extremity of each fibre is connected with the peripheral extremity of a single nervous fibre only, and that this peripheral extremity is in relation with only one point of the brain or spinal cord; so that, corresponding to the many millions of primitive fibres which are given off to peripheral parts of the body, there are the same number of peripheral points of the body represented in the brain. If, on the contrary, the primitive fibres anastomose with each other in their course within the small fasciculi, and in the frequent anastomoses and plexuses of the nerves themselves, and do not merely lie in apposition; then the cerebral extremity of a nervous fibril will be in relation with

very many peripheral points, the number of which will be equal to the number of primitive fibres which have coalesced; and, since the nerves are seen to anastomose in all parts of the body, there would, if the primitive fibres likewise anastomosed, be scarcely a single point of the body represented isolated and distinct in the brain; the irritation of a primitive fibre in a single point of the skin would necessarily be propagated through all the anastomoses,—in other words, no local impression on a single definite point would be perceived by the brain; for the sensation of a single point evidently depends on the impression being conveyed by means of a single fibre to a single point of the sensorium. It is very clear, that if the anastomoses of the nerves in the transmission of the nervous principle had the same influence as the anastomoses of vessels, no local nervous influence could be communicated from the brain to the peripheral parts, nor from the latter to the brain. The possibility of our establishing an accurate theory of the action of the nerves rests wholly on the question of the primitive nervous fibres anastomosing, or not.*

Fontana, and afterwards Prevost and Dumas, observed, that the primitive fibres of nerves enclosed in a fasciculus do not unite with each other, but merely run side by side. At that period, however, physiologists had scarcely a suspicion of the importance of this fact for the theory of nervous action. Some years ago, at the time that I made known my experiments on the motor and sensitive roots of the nerves, I took up the enquiry. Of course, only a certain length of nerve can be examined under the microscope at a time; but by examining successive points along the course of the nerve, we may arrive at a more certain conclusion as to the existence, or not, of anastomoses between the primitive fibres. I have in this way examined with the simple microscope the primitive fibres of a nervous fasciculus spread out on a black surface, but have never seen two fibres unite into one: they always were seen to continue separate, whether they lay side by side, or crossed the one over the other; and, even when two fasciculi have united, I could perceive no actual union of the fibres,—these remained evidently quite distinct, and were merely in juxtaposition. It is evident, from the external appearance of the nerve before and after such an anastomosis of fasciculi, that such must be the case. If the primitive fibres themselves united, forming a smaller number of fibres by their union, the size of the fasciculus resulting from the anastomosis of two, ought to be the mean between the two uniting fasciculi, which is not the case; except in the instance of the sympathetic nerve, the fasciculus resulting from an anastomosis always equals exactly the size of the two, which united to form it, taken together. When nerves form a plexus, the nerves which issue from it, however great the interlacement of fibres may have

* [Similar arguments in favour of the insulated course of the nervous filaments were advanced more than seventy years ago by Dr. Whytt. (See Whytt's works, p. 505.)]

been, will always form as large a mass as those that entered it. The same law prevails in the ramification of nerves; a nerve, after having given off a branch, is thinner in exact proportion to the number of fibres in the branch which has left it; and by the aid of minute dissection it is easily seen that when a branch is given off, the fibres in the trunk do not divide each into two, one remaining in the trunk while the other leaves it to join the branch, but that the fibres of the branch are some of those which already existed in the trunk: hence, in a nerve, very different fibres, sensitive and motor, may be associated together, and in the trunk of a nerve there may even be branches contained which do not unite with the other constituent fasciculi, and have no resemblance to them in its properties. Thus the nervus mylo-hyoideus, a motor nerve, is commonly regarded in a general way as a branch of the inferior dental, a nerve of sensation, although these two nerves have nothing in common except their position side by side; and of this there are frequent examples. We hence see that the properties of the component fasciculi have nothing to do with the nature of the trunk of the nerve itself; but that, on the contrary, the nervous trunk, particularly at some distance from the brain, may be constituted of fasciculi of very various properties, the different fasciculi destined for a particular limb having become annexed to it in its course.

The view here given of the course of the primitive nervous fibres from the brain to their ultimate termination, is opposed to the statement that the nerves increase in size in their course, which, however, is an error originated by Soemmering. The nerve is certainly smaller before it passes through the dura mater, and receives its neurilema, than it is afterwards; but, when invested by its neurilema, its diameter does not vary as long as it gives off no branches. The branches in every case contain the same mass of nervous substance as the trunk from which they arise; if there is a slight difference, it is owing to the quantity of neurilema in the branches being greater. These remarks on the ramification of nerves, apply also in the case of a plexus formed by two different nerves. Some years ago I examined, with the most careful dissection, the anastomoses of the facial with the infra-orbital nerve in the rabbit and sheep; and convinced myself, by accurate drawing of the course of the primitive fibres of both, that the fibres merely attach themselves to one another, and arrange themselves in new fasciculi. With these principles, therefore, we must regard the primitive fibres of all the cerebro-spinal nerves as isolated and distinct from their origin to their termination, and as radii issuing from the axis of the nervous system. Strictly considered, these radii issue from the spinal cord in a nearly continuous line on each side; but a certain number of them are collected at intervals into a fasciculus for the convenience of their distribution to the peripheral parts.

The foregoing results of my own observation I have taught for several years in my lectures. In the year 1830 I had an opportunity to communicate them in conversation to Prof. Van der Kolk, of Utrecht, when I begged him to put my observations to the test. The views which I had adopted, and which agree with those of Fontana and Prevost, have recently received confirmation in my mind from my illustrious colleague, M. Ehrenberg, having verified the observations on which they rest. The subject has been treated very fully by Kronenberg.*

The above statements refer merely to the white fibres of the cerebro-spinal and sympathetic nerves; for it is probable that the grey fibres may be connected with each other (at all events, through the medium of the ganglia).

Mode of termination of the nerves.—This is a subject, the investigation of which has occupied Treviranus, Gottsche, Valentin, Emmert, the younger Burdach, and Schwann. The principal question to be decided is, whether the nervous fibres terminate by uniting with each other, or remain isolated even at their extremities. It is found that the nervous fibres terminate either by the formation of regular anastomosing loops between every two fibres; or by uniting so as to form a network like blood-vessels; or thirdly, they all terminate in an isolated manner without being connected together. The first was observed by Prevost, Dumas, Valentin, and Emmert to be the mode of termination of the nerves in the muscles; and by Breschet, Valentin, and Burdach it was observed in the case of the nerves of sensation: the second, or reticular mode of termination, was seen by Schwann in the mesentery of the frog and fire-toad (rana bombina), and in the tail of the larva of the toad: the third was discovered by Treviranus in the eye and ear, and the observation is confirmed by Gottsche.

It appears that Prevost and Dumas have not examined the primitive nervous fibres themselves in the muscles; in which, however, Valentin† and Emmert‡ have found the loop-like connection of the nervous fibres to exist. This mode of termination of the primitive nervous fibre has been observed by Valentin in the iris and ciliary ligament likewise, in the ampulla (Flasche) of the cochlea of birds, in the auditory folds or rugæ of the cochlea of birds, in the ampullæ of the semicircular canals, in the follicle of the tooth, and in the skin of the frog. It was seen, moreover, by Breschet in the cochlea and in the ampullæ of the semicircular canals, and in his earlier observations in the papillæ of the skin. The loop-like connection of one primitive nervous fibre with another was observed also by the younger Burdach in the skin of the frog, and the loops seemed to him to be formed even between fibres coming from different

* Plexuum Nervorum structura et virtutes. Berol. 1836.

† Nov. Act. Nat. Cur. xviii. p. 1, 51.

‡ Ueber die Endigungsweise der Nerven in den Muskeln. Bern, 1836. iv.

branches.* It is not very probable that the so-called primitive fibres, which are of considerable size, form the actual termination of the nerves, in parts of which the ultimate elements are much more minute than them. Schwann indeed has seen in the mesentery of the frog, issuing from the so-called primitive fibres, numerous finer filaments, which here and there presented small ganglia, from which again several twigs were given off. Further researches on the mode of termination of the nerves in the tail of the larva of the toad have confirmed these observations. The nervous fibrils resulting from the splitting of fibres, of the size of what are ordinarily termed primitive fibres, are excessively minute, and are destitute of the dark tubular sheath which invests the ordinary primitive fibres. The minute ganglia are nearly constantly present. From the minute fibrils just described, and from the ganglia on them, still more delicate threads are given off, and terminate by forming a network.

In the retina, and in the ear, the nervous fibres terminate in an isolated manner, without uniting with each other. The layer of the retina formed of the nervous fibres, and the more internal so-named granular layer, were known to Fontana. There is likewise an external layer composed of granules disposed in a pavement-like manner, resembling mosaic work. The nervous fibres, therefore, lie in the middle layer. Treviranus has discovered that the fibres of this layer are, at a certain point of their course, bent from the horizontal direction, and turn towards the inner surface of the retina. Immediately after they have made the turn, they pass through the openings of a vascular network, which is connected with the central vein of the optic nerve. Before they reach the inner surface of the retina, the fibres perforate a second network of vessels, which is formed by branches of the arteria centralis retinæ. Having passed this, they are received into sheath-like processes of the vascular layer of the retina; and, covered by these, terminate on the exterior of the vitreous humour in the form of papillæ. The transverse diameter of one of the nervous fibres of the retina was, in the hedgehog, 0·001 millim. [or $\frac{1}{2116}$ of an English line.] The diameter of the papillæ in the rabbit 0·003 millim. [$\frac{1}{715}$ of an English line.]

The diameter of the papillæ in birds was from 0·002 to 0·004 millim. [from $\frac{1}{1058}$ to $\frac{1}{530}$ of an English line.] In the frog, the fibres measured 0·0044; the papillæ, 0·000066 millim. in diameter, [from $\frac{1}{486}$ to $\frac{1}{324}$ of an English line]; in the crucian the diameter of the latter was from 0·0039 to 0·004 millim. [$\frac{1}{542}$ to $\frac{1}{530}$ of an English line.] The bodies which Treviranus regards as the ends of the nervous fibres bent inwards, are short cylinders which separate very easily from the subjacent layer. They are easily seen in perfectly fresh eyes of quadrupeds; their existence has been confirmed by Gottsche, Ehrenberg, Volkmann, and

* Dr. Ernst Burdach, Beitrag zur Microscop. Anat. der Nerven. Königsb. 1837.

Weber, as well as by myself. But whether each of the bodies in question is the end of one fibre only, or whether several rest on one fibre, is not yet quite certain. A few hours after death their proper form is no longer perceptible, and in their place there are merely granules, which has given rise to the incorrect notion of the existence of an internal granular layer of the retina. The papillæ of the cylinders do not appear to be distinct, except in fishes, in which Gottsche* has described them.

Treviranus observed the papillar mode of termination of the nervous fibres, not merely in the retina, but also in the case of the auditory and olfactory nerves; and here the papillæ were more thread-like. Those of the auditory nerve he saw on the lamina spiralis of the cochlea in young mice. The bony portion was wholly covered with thread-like papillæ crowded closely together. The nervous fibres ran towards the membranous border of the lamina spiralis under the surface of the membrane, more widely separated from each other; and, after having made spiral convolutions in the canals which contained them, issued through minute foramina in the form of globules of the diameter of 0·0016 or 0·0033 millimeter, [about $\frac{1}{1322}$ to $\frac{1}{641}$ of an English line,] which is likewise the size of the cylindrical fibres of the auditory nerve themselves. In dissecting these parts in the fox, Treviranus found that the nerves of the semicircular canals on reaching the ampullæ, spread out into a lamella on each side of the sac, becoming divided into more minute fibrils, which unite again into larger fibres before leaving the lamella. The fibres of the nerve of the cochlea in the hare and rabbit, and those of the auditory nerve of fishes, have, according to Gottsche, club-like terminations. On the spiral lamina of the cochlea of birds, which was described by Windischmann, the nervous fibres appear to me to be likewise distinct, and not to unite with each other. The principal mass of the nerve of the cochlea runs here at one border of the cartilage of the cochlea, and spreads itself out very regularly in the substance of the cartilage; while fibrils much more minute issue from the cartilage, and, running parallel and close to each other, extend over the greatest part of the breadth of the extremely delicate lamina spiralis.

The mode of termination of the fibres of the brain has been investigated by Valentin. The primitive fibres of the spinal nerves do not end in the spinal cord; they continue their course as far as the brain. The fibres of the nerves of the extremity of the spinal cord run forwards, while those of the nerves which enter the spinal cord laterally at its upper part pass first transversely towards the interior of

* Pfaff's Mittheilungen aus dem Gebiete der Medicin, Chirurgie und Pharmacie. 1836. Heft 3, 4. Heft 5, 6. For an account of the observations of other anatomists, see Müller's Archiv. 1837. Jahresbericht [partly translated in the British and For. Med. Review for January 1838].

the cord, as far, or nearly as far, as the grey substance, and then follow the same longitudinal course to the brain as the others. In the white substance, the fibres lie in contact with each other; but, at the line of contact of the white and grey substances, the fibres become separated by the globules of grey matter, which we shall presently describe, and at length radiate out into the cortical substance, where they form loops by uniting one with another. This is seen most distinctly where the white and reddish grey substances are united together, or in the yellow substance at the periphery of the hemispheres of the cerebrum and cerebellum.

Grey substance of the brain, spinal cord, and ganglia.—In the interior of the ganglia of invertebrate animals, (the leech and common slug,) Ehrenberg has observed club-shaped bodies, which in the ganglia of the leech form eight fasciculi, every two of which are continued into one of the four arms of the ganglia by means of long cylindrical tubes. In the enlarged part of these club-like bodies is a nucleus; and, besides this, there are in the leech several other little globules (it is so represented in the engraving in Ehrenberg's paper). Valentin has described similar bodies as existing in the ganglia of the abdominal cord of the leech. He saw globules which, like those of the ganglia of the higher animals, contained a nucleus. In this nucleus there was, at a point close to the surface, a reddish body, and sometimes, in place of this, there were several smaller corpuscules. Purkinje has seen similar caudate bodies in the yellow mass between the cortical and medullary substance of the cerebellum. He describes them as having a bright nucleus in the interior, and, corresponding to this, a smaller one on the surface. They are arranged side by side; their rounded extremity turned towards the white substance, their tail-like prolongations towards the cortical substance. As similar to these I regard certain club-shaped nucleated bodies which I have found in the medulla oblongata of the cyclostomatous fishes (in a petromyzon preserved in spirit). But the latter were of peculiar form: their thick extremity was not rounded, but generally dentated; in most cases, it sent out several,—two, three, or four, tooth-like processes, the form and relative position of which varied very much.*

The elements of the ganglia of the nerves in the higher animals, and in the human subject, have been ascertained by Valentin to be globules of considerable size, which differ from the above described club-shaped bodies merely by their more spherical form, but have like them a nucleus, and in the circumference of this another smaller nucleus, and frequently also spots of pigment on their surface. One or more fasciculi of fibres which enter the ganglion form within it a plexus, the fibres undergoing a different arrangement, and again issue from it; while single fibres, or

* See Müller's Archiv. 1837. p. xvii. Jahresb.

fasciculi of fibres form an interlacement around the globules of the ganglion. The fibres which form this interlacement come off from the trunk of the nerve, and join it again. This description, in fact, applies to the ganglionic globules generally, as may be easily verified.

The grey substance of the brain and spinal cord is, according to Valentin, formed wholly of the same globules as the ganglia of vertebrate animals. The appearance of minute granules is produced by the disintegration of the original globules, which are very soft. The only circumstance in which the globules of the grey substance of the brain differ from those of the ganglia, is that the cellular tissue which invests the former is less firm. In the white substance of the brain there are, according to Valentin, no globules or granules; the appearance of granules in it is produced by the nervous fibres being broken up. On the quantity of the deposit of grey globules depends the degree in which certain parts of the brain differ in colour from the white or fibrous substance: where the primitive fibres are in greatest number, the colour is whitish grey; where they are less abundant, it is reddish grey: the darker colour of certain portions of the brain depends on a pigment deposited on the globules.

In the spinal cord there are, as Rolando discovered, two kinds of grey substance. That which is commonly known as the grey substance of the spinal cord, is called by Rolando* "substantia cinerea, spongiosa, vasculosa." At the posterior part of the posterior cornua of this substance runs a line of perfectly grey matter, called by Rolando the "substantia cinerea gelatinosa." The first contains, according to Remak, the great ganglionic globules above described, together with numerous fibres; the latter, on the contrary, contains corpuscules similar to the red particles of frog's blood. The continuation of the substantia cinerea gelatinosa in the medulla oblongata, where it comes to the surface, has the same structure.

It would be important to know whether the large globules of the grey substance in the brain and in the ganglia have, or have not, any connection with other parts or with one another. Certain processes, which are, under favourable circumstances, seen issuing here and there from the globules, suggest the probability that they are connected with each other by fibres. I saw these tooth-like processes first on the club-like bodies in the medulla oblongata of the petromyzon. Remak observed them soon afterwards on the globules of the grey substance of the brain and ganglia. He not only saw fibres coming off from the surface of the globules of the ganglia, but succeeded even in isolating them to the extent of several or many times the diameter of the globules. These fibres of the ganglionic globules have some similarity with the delicate

* Saggio sopra la vera struttura del Cervello; edit. 2. t. ii. Torino, 1828. Tab. iii. fig. 2. 3. sp.

grey filaments which Remak has observed in ganglionic nerves; and if the latter filaments which form the grey fasciculi of the sympathetic are organic fibres, it becomes in some degree probable, or at least possible, that this is the origin of the grey fibres of the organic nerves.

Distribution of the white and grey systems of fibres in the cerebro-spinal and sympathetic nerves.—We have already mentioned that the cerebro-spinal nerves contain some fasciculi of grey fibres, and that the sympathetic contains likewise some few fasciculi of white fibres; we have lastly suggested as probable, that the grey fibres, which have a peculiar structure, derive their origin from the ganglionic globules which are so frequent in the ganglia of the sympathetic, but which are present, though in less number, at those parts of the cerebro-spinal nerves, where the fibres of the sympathetic enter more largely into their composition, as at the angle of the facial nerve where it is joined by the vidian, and in the second and third branch of the nervus trigeminus. We see therefore that the sympathetic differs only in a relative manner from the other nerves. The mixed cerebral and spinal nerves contain chiefly fasciculi of sensitive and motor fibres, and a few fasciculi of grey fibres which have a tendency to the formation of ganglia; the sympathetic, on the contrary, contains a few sensorial and motor elements derived from the posterior and anterior roots of the mixed nerves, and consists chiefly of grey organic fibres, corresponding with its distribution to parts which serve principally for the production of chemical changes in the fluids of the body. Hence the frequency of ganglia in the sympathetic nerve; while in the cerebro-spinal system of nerves, if we except the regular ganglia of the posterior roots, ganglia are rare, occurring only where there is a considerable intermixture of grey fibres from the sympathetic.

Classification of the ganglia.—The ganglia of the nerves may be arranged in three classes:

1. *Ganglia of the posterior roots of the spinal and cerebral nerves, the ganglion of the larger portion of the nervus trigeminus, that of the vagus, the ganglion jugulare superius of the glosso-pharyngeal nerve, and lastly, the ganglion on the small posterior root of the hypoglossal nerve.*

These ganglia have the common character of belonging to nerves of sensation: we shall show at a future page that the posterior roots of the spinal nerves are sensitive, not motor. The ganglion of the first spinal nerve sometimes, and those of the two last always, present anomalies in respect to position. The first is sometimes situated within the dura mater;* the two last very delicate spinal nerves have their ganglia always in the cavity of the dura mater.† The portio major nervi trigemini, which expands into the Gasserian ganglion, bears the same

* Mayer, Nov. Act. Nat. Cur. v. xxi.

† Schlemm, Müller's Archiv. 1834. i.

relation to the portio minor as the posterior to the anterior roots of the spinal nerves. Goerres* was the first who compared the nervus vagus and the nervus accessorius to the posterior and anterior roots of a spinal nerve. The ganglion of the vagus in the foramen jugulare must certainly be regarded as a ganglion of a sensitive nerve, although in some animals several fibres of the vagus pass the ganglion without forming part of it. Santorini observed the existence in some cases of a posterior root (without a ganglion) to the hypoglossal nerve; and Mayer† has discovered that in several mammalia (the ox, dog, and hog,) the hypoglossal has an extremely delicate posterior root arising from the posterior surface of the medulla oblongata, passing over the nervus accessorius without being connected with it, and forming at that point a distinct ganglion. A thicker nervous cord issues from the ganglion, and, piercing the first process of the ligamentum denticulatum, (or, as we recently observed, passing above it,) goes to join the known anterior root. Mayer has hitherto found this posterior root and ganglion but once in the human subject.

I have observed‡ a similar fact with regard to the origin of the glosso-pharyngeal in man, — namely, that, besides the ganglion petrosum at the inferior opening of the foramen lacerum, there is a very small ganglion at the posterior and external side of the root of this nerve, and at the upper or cranial extremity of the foramen lacerum. This little ganglion cannot be seen until the dura mater around the opening is removed, and the posterior border of the os petrosum chiseled away. It does not involve the whole root; but only a fasciculus of fibres, which is larger after passing through the ganglion, but has not a different origin from the rest of the nerve. Ehrenritter§ first discovered this ganglion, but he did not observe its special relation to the fibres of the glosso-pharyngeus; and I pointed out the resemblance of the origin of the nerve to that of the trigeminus, and that both are mixed nerves like the spinal nerves.

The other much longer known ganglion of the glosso-pharyngeus, the ganglion petrosum, would seem not to be analogous to the ganglia of the sensitive nerves, but rather to those enlargements of nerves which are sometimes observed at the points where branches of the sympathetic unite with them,—such as, for example, the enlargement of the facial at the angle where it is joined by the superficial branch of the vidian or chorda tympani. In fact, the ganglion petrosum is connected with an ascending branch of the superior cervical ganglion, and by means of the ramus tympanicus ganglii petrosi with the ramus carotico-tympanicus of the sympathetic.

* Exposition der Physiologie. Coblenz. 1805. 328. † Loc. cit.

‡ See the Medizin. (Vereins.) Zeitung. Berlin, 1833. No. 52.

§ Salzburg. Med. Zeit. 1790. Bd. iv. p. 319.

The structure of the ganglia of this class is not essentially different from that of the ganglia of the sympathetic; but we see in them more distinctly the pencil of fibres passing through unchanged between the globules of the proper substance of the ganglion. The special function of the ganglia of the sensitive roots is not yet known. Perhaps they give rise to the organic fibres of the sympathetic, which these ganglia would then connect with the posterior columns of the spinal marrow. The sensitive and motor white fibres of the sympathetic are connected with the posterior and anterior roots of the spinal nerves. The question, therefore, arises whether the posterior roots of the spinal nerves connect both the sensitive and organic fibres with the spinal marrow. The ganglia of the sympathetic itself, however, appear to be at all events a principal source of the organic fibres. The lateral cords of the sympathetic are proportionally much whiter than the branches of the great abdominal ganglia.

The facts which we have at present considered do not enable us to decide whether an increase in the number of fibres takes place in the ganglia of the sensitive roots, and in the Gasserian ganglion. The white fibres pass through with merely a change of arrangement; thus far is certain. But grey fibres may arise from the ganglionic globules, since it is indeed a known fact that grey fasciculi arise in the Gasserian ganglion, and accompany the branches of the nervus trigeminus.*

2. *Ganglia of the sympathetic nerve.*—It is so difficult a matter to ascertain what becomes of the nervous fibres in these ganglia, that we have, in fact, not the least knowledge on that point. The main question here, as in other parts of the nervous system, is, whether the primitive fibres really unite together, or merely lie in juxtaposition, and form interlacements with others; or whether the primitive fibres divide in the peripheral direction being thus multiplied. If a multiplication of fibres takes place in any ganglia, it is certainly most likely to be in the ganglia of the sympathetic; and it is, at least, very difficult to suppose that all the primitive fibres of the abdominal plexus are contained in the roots of the sympathetic from the spinal nerves. But if this multiplication does take place, it can affect only the delicate grey organic fibres; for the ordinary primitive fibres of the nerves are known to pass unchanged through the ganglia of the sympathetic, as through those of the posterior roots of the spinal nerves.

The ganglia of the sympathetic form two series. The first consists of those which lie along each side of the spinal column at the points where the roots of the sympathetic nerve, coming from the spinal nerves, unite with the longitudinal cord of the sympathetic: it comprehends, therefore, all the cervical, intercostal, lumbar, and sacral ganglia. To the

* See Wutzer, de Gangliorum Fabricâ. Berol. 1817.

second series belong the sympathetic ganglia situated in the middle line, or the plexiform ganglia in the plexuses of the abdomen.

3. *Ganglia of the cerebro-spinal nerves at the points where they unite with branches of the sympathetic.*—These are the ganglion petrosum nervi glosso-pharyngei, the intumescentia gangliiformis on the angle of the facial nerve, the ganglion spheno-palatinum on the second branch of the nervus trigeminus, the ciliary ganglion, and perhaps, also, the otic ganglion, and some others. Ganglia are not always formed, however, where fibres of the sympathetic unite with fibres of the cerebro-spinal nerves; on the contrary, it happens very rarely; for at not one of all the numerous points of origin of the sympathetic from the cerebral and spinal nerves is there a ganglion formed. The reason why, in the instances above mentioned, the union of fibres of the sympathetic with cerebral nerves is attended with the formation of a ganglion on the latter, appears to me to be that, in these cases, branches of the cerebral nerves coming from the brain are not given off to the sympathetic, but that branches of the sympathetic here join the cerebral nerves; the fibres thus added to the nerves being continued then, not merely to the brain, but in the peripheral direction with the cerebral nerve. If this supposition was of general application, we should know, when a cerebral nerve, not at its root, but in its further course, presented a swelling corresponding with the point of union with the sympathetic, that the fibres of the sympathetic joining it did not come as roots of the sympathetic from the cerebral nerve, but were fibres of the former going to join the latter. Thus in the ciliary ganglion there is a mingling of fibres of the nasal branch of the fifth nerve, of the branch of the third nerve to the inferior oblique muscle, and of the sympathetic; the object of which is not to give new roots to the sympathetic, but to bring into the ciliary nerves fibres of the sympathetic, with sensitive fibres of the first division of the fifth, and motor fibres of the third nerve. The same is the case with the spheno-palatine ganglion on the second division of the fifth nerve; for this ganglion—since the sympathetic is, according to Bendz, connected with the trunk of the fifth in the Gasserian ganglion through the medium of fibres from the otic ganglion—would appear not to afford roots to the sympathetic merely, but to receive fibres from the sympathetic for the purpose of distributing them with the branches of the second division of the fifth. In fact, Retzius has in the horse distinctly seen these fibres of the sympathetic continued from the spheno-palatine ganglion in the peripheral direction on the second division of the fifth nerve, and has described them in the Isis for 1827. I have seen the same in the ox. The ganglion petrosum is, as I have endeavoured to show above, not the ordinary ganglion of a sensitive nerve, since the small ganglion which I have observed on the glosso-pharyngeal nerve at a higher point stands in that relation to it; the

ganglion petrosum arises from the union of several branches of the sympathetic with the nerve at that point. At present, the correctness of this view cannot be quite decided; but it may be of service at a future period in deciding which of the numerous connections of the sympathetic with the cerebro-spinal system are its roots, and which its peripheral branches given off to the spinal nerves.

Should the above view be confirmed, then the ganglia in question,—those just considered,—will no longer be a distinct class; but will belong to those of the sympathetic system, and will be included in the second class. The sympathetic system would in that case have three kinds of ganglia.

1. The ganglia of the middle line, or the plexus-like ganglia of the abdomen.

2. The ganglia of the lateral cords, lying at the points of junction of the roots of the sympathetic.

3. The ganglia of the sympathetic, which are situated at the points of junction of this nerve with the cerebral nerves, and which modify the properties of the latter, not those of the sympathetic.

CHAPTER II.

OF THE EXCITABILITY OF THE NERVES.

The laws of animal excitability in general have been considered in the Prolegomena on General Physiology (page 51).

This property of organised bodies,—excitability,—is also possessed by the nerves, both the general and special endowments of which are in every instance manifested under the influence of stimuli. Physiologists have not however merely to ascertain the laws governing this general property, which, unfortunately, was the sole object that occupied the attention of Brown and his followers; but to investigate the peculiar forces themselves which are susceptible of this excitation, and in this there is a great field opened for experimental science. In inquiring into the nature of the forces resident in the nerves, it is necessary to study the action of all kinds of stimuli upon them,—a method of inquiry which acquires for physiology an experimental certainty similar to that which the sciences of physics and chemistry in reference to inorganic bodies enjoy. In chemical processes, reagents give rise only to products, combinations, and decompositions; applied to organic bodies, and especially to the nerves, their effects, however various they themselves may be, are never other than manifestations of the proper forces of the bodies acted on, or modifications of their forces. It will be seen that all influences acting on the nerves either excite them, or produce an altered state of their excitability; in the first case, all stimuli, however different they may be from each other, act in the same manner; the

most different causes produce the same effect, because that on which they act possesses but one kind of excitable force, and because agents in themselves the most different act here by virtue of the same quality, that of stimuli.

1. *Of the action of stimuli on the nerves.*

All stimuli, as well the internal organic as the inorganic,—chemical, mechanical, caustic, and electro-galvanic,—when applied to parts endowed with sensation, or to sensitive nerves, the connection of the latter with the brain and spinal cord being uninjured, produce sensations. All these different stimuli resemble each other in this respect,—that a certain degree of their action produces merely the phenomena of sensation, while their more violent action induces changes in the force on which the sensibility depends. All stimuli, organic and inorganic, applied to the nerves of muscles, or to the muscles themselves, excite contraction of the latter; and this effect is produced, as well when the nerve is still in connection with the brain, as when its communication with the nervous centres is cut off. Nerves, therefore, have by virtue of their excitability the property of exciting contractions in muscles to which they are distributed; and this they do as long as the muscles preserve their vitality, and as long after death as the nerves retain their excitability. For the production of contractions in a muscle, by irritating its nerve, it is necessary that the latter shall not have lost its integrity between the point irritated and the muscle, although its connection with the brain or spinal marrow may not be preserved; while, on the other hand, all stimuli produce sensation in a nerve, whether it be entire or mutilated, as long as the portion irritated maintains an uninterrupted communication with the spinal cord or brain.

a. Mechanical stimuli.—Every kind of mechanical irritation,—stretching, compression, or puncture,—excites in sensitive nerves, under the conditions already mentioned, sensations; provided the mechanical influence,—for instance, the compression,—is not so violent as to destroy the power of the nerve. Sensation ensues whenever the extremities, branches, or stump of a divided nerve are irritated, if the connection of the nerve with the brain and spinal marrow is not interrupted. Mechanical irritation of the sensitive nerves of the trunk, and of their divisions, produces merely the varieties of common sensation, namely, pain, and the sensation of touch; irritation of the nerves of sight and the retina, on the contrary, gives rise to no pain, according to M. Magendie, but to the perception of light, as we know from common experience of the effect of pressure or a blow upon the eye. Mechanical impressions on the auditory nerve, such as are produced by the vibrations of sonoriferous media, or the jarring of the head and ear in long journeys, give rise to the sensation of sound, but not to pain, of which it appears that the auditory nerve is not susceptible.

So also, if with a needle we tear, prick, bruise, drag, or stretch a nerve distributed to a muscle, contraction of the latter is produced, and indeed as powerful a contraction as is excited by any galvanic or electric influence. The part of the nerve which is connected with the muscle will still retain this power, however much we may curtail it; but irritation of the other portion of a divided nerve, that which is in connection with the spinal cord and brain, never excites contractions of the muscles.

Mechanical irritation, when so violent as to injure the delicate texture of the primitive nervous fibres, deprives the nerves of their power of producing sensations, when irritation is again applied at a point more distant from the brain than the injured spot: in the same way, no irritation of a nerve distributed to a muscle is capable of exciting contraction of the latter, if the nerve has been compressed and bruised between the point of irritation and the muscle; the effect of such an injury is the same as that of division. The sensitive power of a nerve, therefore, is interrupted by any mechanical destruction of its texture between the brain and the part stimulated; and the motor power by the same injury affecting it between the irritated part and the muscle. But the mechanical injury produced by pressure destroys the power of the nerve only locally; irritation applied at any point between the injured part and the brain excites sensation; at any point between the injured part and the muscles, contraction of the latter. If, however, the nerve of a muscle is stretched violently in its whole length, it frequently loses its excitability to the same extent; and even the muscle sometimes in this case loses its irritability, and can be made to contract by no manner of stimulus.

b. Temperature.—Heat and cold likewise excite sensation, and contraction of muscles.

When heat is applied to the nerve going to a muscle, or to the muscle itself, contractions of it are produced; these are very violent when the flame of a candle is applied to the nerve, an experiment which I have performed both in frogs and rabbits: less elevated degrees of heat,—for example, that of a piece of iron merely warmed,—do not irritate sufficiently to produce contractions of the muscles.

The application of cold has the same effect as heat; thus it is an old observation, that violent contractions of the muscle immediately ensue when cold water is injected into its artery; cold water applied to the surface of a muscle likewise causes it to contract. This action of cold on muscles has been taken advantage of in the practice of medicine; thus, in cases of atony of the uterus, and of uterine hemorrhage after delivery, cold water has been injected into the vessels of the still adherent placenta.

Sympathetic contractions of the iris are produced by drawing cold

water into the nostrils. Great degrees of cold and heat, whether their application is sudden or gradual, destroy the nervous energy, and give rise to death or asphyxia. The effect of cold or heat very gradually increased is sometimes to reduce the excitability to a latent state, producing the hybernation and summer sleep of certain animals.

The effect of the local action of an excessive degree of artificial cold or heat on the nerves, is the same as that of destructive mechanical irritation. The sensitive and motor power in the part is destroyed, but all the other parts of the nerve retain their excitability; and, after the extremity of a divided nerve going to a muscle has been burnt, contractions of the muscle may be excited by irritating the nerve below the burnt part: of this I have convinced myself by experiments on frogs and rabbits.

c. Chemical stimuli.—All chemical irritants excite the sensitive power of the nerves as long as the connection of the latter with the brain and spinal cord has suffered no interruption. Alkalies excite contractions of the muscles likewise when applied to their nerves; many other reagents, particularly the acids and metallic salts, for example, the mineral acids,— sulphuric, nitric, and muriatic acids, bichloride of mercury, and muriate of ammonia, and moreover alcohol, do not excite the slightest contraction of the muscles when applied to the nerves, but must be applied to the muscles themselves. All these substances in a concentrated state destroy the power of the nerve at the point to which they are applied, so that irritation by other stimuli is incapable of exciting their motor action, unless applied between the injured spot and the muscles. All the substances named have likewise a destructive action on the muscular substance, but excite contractions at the moment of their application; the last effect is least marked in the case of alcohol, though I have perceived it some few times in rabbits.

The most violent contractions of the muscles, often much stronger than those produced by the galvanic influence of a single pair of plates, are excited by touching the nerves with alkalies. I, as well as the Baron A. von Humboldt, have seen this effect from caustic potash. Humboldt* has seen the tremor of the muscles continue forty or fifty seconds. He likewise observed that the twitchings of the muscles were produced, although one or more ligatures had been placed on the nerve. In this case the ligatures formed a conducting medium for the alkali. Humboldt could produce no contractions by means of acids; the only substances which, according to him, excite contractions of the muscles when applied to the nerves, are potash, soda, ammonia, opium (?), muriate of barytes, arsenic acid, tartrate of antimony, alcohol (?), and chloric acid (?). I have seen no twitchings of the muscles follow the applica-

* Versuche über die gereizte Muskel-und Nerven-faser. Posen, 1797. Bd. ii. p. 363.

tion of the two last-mentioned substances to the nerves themselves; nor of opium alone, in the state of watery solution. Humboldt employed the tincture of opium, so that the effect might have been owing to the spirit; but yet, in one experiment which I performed with the tincture of opium, no contractions of the muscles were excited. Chemical irritants introduced into the blood likewise act on the excitability of the nerves. Thus, it is well known that emetic substances introduced into the blood-vessels produce the same effect as when taken into the stomach; tartar emetic and muriate of barytes applied to wounds excite vomiting.*

d. Electric stimuli.†—Electricity produces in the nerves the same phenomena of reaction that follow the application of mechanical and chemical stimuli. Mechanical violence, as in striking the ulnar nerve at the elbow, gives rise to the sensation of a shock; the same sensation is felt when an electric discharge is passed through a nerve. This effect must be regarded merely as a sensation; a mode of reaction of the nerve, with which its cause, the electricity, must not be confounded. The sensation of the blow or shock is not the action of the electricity, but is the action of the nerve, which becomes the seat of this sensation whenever a violent change is produced in the state of its component parts, whether this change is produced by animal or mechanical stimuli, or by electricity.

The discovery of galvanic electricity in 1790 has been the occasion of the excitability of the nerves being more investigated, namely, by the application of the stimulus of electricity to individual nerves; but in this important agent we have not become acquainted with a fluid similar in its action to the nerves, but merely with a new stimulus of the nerves in addition to those already known. Different metals, and many other bodies, even animal substances of heterogeneous composition, when brought into contact, are thrown into a state of electric tension, which ceases when the two bodies are brought into communication at other points by a conducting substance, that is to say, when the circle is closed, the equilibrium being then restored; and if a reagent for electricity forms part of the circle, the phenomena peculiar to electricity ensue. The leg or any other muscular part of a frog or other animal lately killed being separated from the body, the muscles laid bare, and the nerve dissected out, but left connected by its branches with the muscles, if the part so prepared be laid upon an insulating plate of glass, and two different metals—for example, zinc and copper,—brought into contact with each other, and at the same time with the nerve and muscle, a contraction of the muscle

* Scheel, Nordisches Archiv. 2. St. 1. p. 137.—Magendie, sur le Vomissement, p. 16-30.—Brodie, Philos. Transact. 1812.

† See the article by J. Müller in the Encyclop. Wörterbuch der Medicin. Wissenschaften.

takes place at the moment that the circle is closed, and frequently also when it is again interrupted. The same effect is produced when the two metals, while in contact with each other, are made both to touch at the same time the nerve or the muscle only. The experiment, as here described, always succeeds. There are many other more simple modifications, however, of the experiments with galvanism, the knowledge of which we owe to the excellent labours of Aldini, Pfaff, Ritter, and above all of Humboldt; but these succeed only when the frogs are in a state of great excitability, namely, before the pairing season, in the cold part of the year after hybernation, and, according to my observation, in the autumn, when the atmosphere begins again to be cold, but not in the summer. These more simple experiments are the most important with reference to the theory of the phenomena produced; they are the following:

1. *Experiments in which the galvanic circuit is not formed.*—Humboldt has discovered, that when the excitability of the frogs is great, it is sufficient that two portions of different or even of the same metal should touch each other, and that one of these be brought into contact with the nerve, no circuit being here formed; and it sometimes happens indeed, though very rarely, (I have, however, myself observed it,) that the frog's limb being very excitable, the mere contact of the nerve with a single homogeneous portion of metal will excite muscular contraction. Pfaff * saw twitchings produced by merely bringing the end of the divided nerve into contact with the surface of quicksilver; and I witnessed the same phenomenon several times on touching the nerve with the point of a pair of scissors, or of a plate of zinc, which I held in my hand, and which consequently was of different temperatures at its two ends. The result here may be explained in the same way as in those experiments in which two different metals are used, if we suppose either that there was a slight admixture in the metal, which was not detected, or that the temperature of the metal was different at different parts; for recent discoveries have shown that a slight difference of chemical composition in the same metal, or a different temperature at its two extremities, is adequate to throw it into a state of electric tension. The effect is facilitated by letting the nerve fall upon the metal. This is to be accounted for, probably, rather by the suddenness of the contact than by the mechanical shock. The latter is not alone the cause of the phenomenon, for Humboldt, Ritter, and Pfaff found that no contraction of the muscles is produced by letting the nerve fall on glass or stone.

2. *Experiments with the galvanic circuit.*—The experiments of this kind also may be reduced to a very simple form when the frogs are in a state of great excitability; it is only in the colder seasons of the year,—in winter, spring, and autumn,—however, that they succeed. Thus,

* Gehler's Physikal. Wörterbuch, iv. 2. p. 709.

contractions of the muscles are sometimes produced, as Humboldt discovered, when the circle is formed of animal substances only, or when it is formed of animal substances and a single metal, the place of the heterogeneous metals being supplied by heterogeneous animal substances.

A. The circle may consist of a single metal with the nerve and muscle of the frog's leg. In this experiment I succeeded very frequently and readily in the spring, before the frogs' pairing time, and in the latter part of the autumn. (See page 69.) The usual effects were produced still more readily when I interposed a piece of the flesh of a frog between the zinc plate and the muscle of the leg, or when my own body formed part of the circle. (Page 69.)

B. The nerve and muscle of the limb may be connected merely by moist animal substance; the nerve, dissected out, being brought into communication with the muscle by means of a separate piece of muscle fixed to an insulating rod of sealing-wax, contractions of the muscles are excited: this was first observed by Humboldt, and I have several times performed the experiment with success. I have made the experiment also in another similar but more complicated manner, closing the circle with my own body, by touching the leg and the nerve of the thigh with my hands, or connecting the leg and ischiadic nerve by means of one or two living frogs, or one or two dead frogs, or by portions of the body of a frog. When sufficient excitability is present, pieces of the body even of a dead and putrid frog are adequate to complete the circle. The same effect is produced likewise, as I have found, by allowing the ischiadic nerve to hang from the leg into a saucer containing blood or water, (it matters not which,) connecting the water and muscles of the thigh by means of a portion of fresh or putrid flesh.

C. Circles of animal substance merely have been shown by Humboldt to excite twitching, when only the nerve of the limb, and not the muscles, are included in the circuit. Humboldt touched the ischiadic nerve with one hand, and at the same time brought a piece of muscular substance, which he held in the other hand, into contact with the same nerve; twitchings of the muscles were produced. When a piece of ivory was used in place of the muscle, no effect, no twitching, followed.

D. Slight twitches of the muscles likewise ensue sometimes, (though this is the experiment which produces them most rarely,) when the nerve is bent back, and made to touch the muscle with which its branches are organically connected.

The first phenomena of this kind were observed by Humboldt. He stripped a frog of its skin, removed all the parts between the pelvis and end of the spinal cord, with the exception of the nerves of the lower extremities, which were therefore connected with the trunk by the nerves alone, and now carried forwards the lower extremity so as to

make the muscle of the thigh touch the nerves just mentioned: violent contractions of the muscles were produced.*

To a similar experiment performed by Galvani, it was objected by Volta, that the contractions of the muscles were the effects of the mechanical stretching of the nerve, and consequently were not to be regarded as a galvanic phenomenon. According to my observation, this is likewise the case in M. Humboldt's experiment; the contraction of the muscles frequently took place long before the nerve and the surface of the limb came into contact. This source of error cannot indeed be well avoided, since the ischiadic nerve winds behind the lower extremity of the pelvis before it reaches the limb; and, in bending the thigh forwards towards the trunk, it is necessarily stretched or extended; and the stretching or extension of a nerve always gives rise to twitches in the muscles to which it is distributed. The same objection may be made to Galvani's experiment, in which the whole spinal marrow must have suffered mechanical violence. It is possible, however, to operate so as to avoid such circumstances. Humboldt, it is true, did not succeed in exciting twitchings of the muscles, after he had separated the nerve from the trunk, by bringing the nerve and muscles of the limb into contact; he likewise failed to excite muscular contractions in another experiment, in which, without touching the muscles, he formed, with a separated portion of nerve, an arch, and with this touched at two points the nerve of the muscle.

The first of these two experiments succeeded, however, frequently in the hands of Pfaff, particularly when the ischiadic nerve was made to touch for a considerable extent the skin of the thigh, not when it was brought into immediate contact with the muscles themselves. I succeeded exactly in the same manner as Pfaff. It was in the spring, before the spawning time; I brought the trunk of the nerve, which was left hanging from the leg, (the thigh having been removed,) into contact with the moist skin of the leg by means of an insulating rod, and contraction of the muscles of the leg followed; the same phenomenon ensued likewise when I separated the nerve again from the surface of the leg. (See page 69.) Here there was a galvanic circle formed, consisting of heterogeneous substances, namely, of nerve, muscle, and skin. Two of these may have been excitors of the electricity, one a conductor merely. An electric current being produced, the nervous principle in the nerve acts as a reagent or electrometer, since when irritated by the electric current it excites a muscular contraction. On the contrary, when the ischiadic nerve is brought into contact with the bare muscles, there are two substances only engaged, which touch each other at two points; there is no third conducting body between the two.

* Humboldt, über die gereizte Muskel-und Nerven-faser, i. p. 32.

The following may be regarded as the *general conditions necessary for the production of muscular contractions by galvanic influence.*

When the galvanic circle is used, there must be three substances,—two excitors of electricity, and one conductor connecting them. The excitors may be heterogeneous animal substances living or dead, such as nerve and muscle, muscle and skin, and so on. The conductor may likewise be a third animal substance, which may be of the same nature as one of the excitors: a portion of a nerve, and the muscle and nerve of the limb in which they are organically connected, are adequate to constitute a galvanic circuit; but the muscle and nerve of the limb, without the aid of a third body, whether similar to one of them or not, are insufficient. The nerve being bent back, and brought into contact with the muscle of the leg, causes no twitchings, unless the skin of the leg remains interposed between the nerve and the muscle; but if a third substance, even though similar in nature to either the muscle or nerve, not organically connected with either, but a separate body, is made to connect them, it is capable of forming with them a galvanic circle, and of exciting muscular contractions: this third substance, we have seen, may be a separate portion of nerve or muscle.

When the electro-excitors are both metals, the nerve and muscle of the limb are at the same time both conductors (like all moist substances) and electrometers, the nervous principle being excited to action by the stimulus of the electric fluid. They constitute an electrometer in this case, in the same way as the inorganic electrometers, for example, the magnetic multiplicator. But the electro-excitors may be animal substances. Thus, the nerve and muscle of the limb, being heterogeneous substances, may become electro-excitors, as well as two heterogeneous dead animal substances; but, inasmuch as they are living, they may, by virtue of the excitability of the nervous principle, act at the same time as an electrometer. When the contractions of the muscles are excited, not by a galvanic circuit, but by the mere application to the nerve of two heterogeneous metals which are in contact with each other, or of a single metal, the nerve must be regarded as an electrometer merely, which indicates the existence of electric tension in two metals of different kinds, or in one metal in a thermo-electric state.

The state of the parts submitted to galvanic action at the periods of closing and opening the circuit, and while the latter is closed, must now be considered. If the positive metal is applied to the nerve, and the negative to the muscle, the contractions generally take place at the moment of closing the circle; and the act of interrupting the circle produces no effect, or only very slight twitches. The result is the same when, both metals being applied to the nerve, the positive is brought into contact with it at a point further distant from the muscle than the negative metal. There are, however, many states of excitement in which the

phenomena are different; first, when the parts still possess the highest degree of excitability, the contraction occurs at the moment that the circle is closed and then only, although the negative metal is applied to the nerve; while, the positive metal being applied to the nerve, the contractions ensue at the moment that the circle is interrupted. In the second state, which is gradually developed from the first, and at length terminates in the loss of all excitability, the application of the negative pole to the nerve, or to the part of the nerve most distant from the muscle, produces contractions at the time of interrupting the circle; while, the position of the metals being reversed, the muscular contractions take place when the circuit is closed: between these two there are other intermediate states in which the contraction takes place equally on the closure and on the opening of the circle, whether the positive or negative metal be applied to the nerve. The results however, according to Pfaff, depend very much on the mode in which the previous experiments on the parts have been performed; if, for example, the circle has remained for a certain time closed, with the negative metal connected with the nerve, the results do not afterwards vary.* This subject has recently been made the subject of investigation by Marianini and Nobili. The supposition of Ritter, that the flexor and extensor muscles are opposed to each other in respect to their susceptibility of the stimulus of galvanism, has not been confirmed.

While the circle is closed, the muscles remain in a state of rest; their excitability only undergoes a change. Pfaff has found that the action of the closed galvanic circle on muscles and nerves is either depressing or vivifying, according to the position of the poles in reference to the muscles and nerve. If the positive metal (the zinc) is applied to the nerve, the irritability of the limb of a frog is lost more rapidly than in another limb not subjected to the galvanic circle; and the greatest degree of excitability can, according to Pfaff, be generally reduced so far that the strongest stimuli do not affect it, by being kept for a quarter of an hour in a circle thus arranged. On the other hand, a circle in which the negative metal (the copper) was connected with the nerve, induced in a short time so high a degree of excitability, that, on opening the circle, the muscles were sometimes thrown into the most violent state of tetanus.

The nerves do not act as mere conductors of the electricity of the galvanic circle. This is proved by the fact that the muscles can be excited to action by applying both poles of the circle to the nerve, so as to direct a galvanic current through it transversely, if the texture of the nerve is sound between the point galvanised and the muscle; but that if, at any intermediate point, its texture has been destroyed by bruising or a ligature applied, the action of the galvanism on the muscles is prevented. Nevertheless, the nerve thus injured is as good a conductor

* Gehler's Physik. Wörterbuch. iv. P. ii. p. 721.

of electricity as before: for if one of the poles of the galvanic circle is applied above the ligature, and the other below it, the electric current passes through the ligatured part; and the nervous principle of that part of the nerve which is situated between the ligature and the muscle being within the circle, and therefore irritated by the electric current, excites the muscles to contract. It is a remarkable circumstance, which Humboldt first observed, that when we wish to excite the contraction of a muscle by applying one pole of the galvanic circle to the muscle, and the other to its nerve which has been previously surrounded with a ligature, there must be a certain extent of nerve left free between the muscle and the ligature; for, if this is applied at a point too close to the muscle, the galvanic current fails to produce any effect till the nerve has been dissected out from the muscle for a certain extent. The effect on the muscles is likewise prevented, even when there is between them and the ligature a free portion of nerve, by surrounding this with some pieces of muscle, wet sponge, or metal. It appears, therefore, that, in the mode of operating mentioned by Humboldt, the nerve between the muscle and the ligature must be insulated.

In all experiments in which the legs of frogs are submitted to galvanism, the contractions of the muscles are stronger in proportion to the length of the nerve going to them (Pfaff). The effect of the galvanic stimulus extends always in the direction from trunk to branches: when both poles of a galvanic circle are applied to a nerve, no contractions are excited in muscles supplied by branches which come off from the nerve at a higher point; but all the muscles are thrown into contraction which receive branches from the nerve below the part galvanised. The strength of the muscular contraction always depends on the number of nervous fibres which lie in the galvanic circle: hence the contraction is most trifling when the muscle only is included in the circle; only that part of the muscle then acts, of which the nervous fibrils were exposed to the galvanic current. Every change in the static condition of the electric fluid seems to become a cause of excitement to the nervous principle: for, according to Marianini, contraction of the muscles is produced not only when the galvanic circle is closed or interrupted, but also by partially diverting the current from the limb; and, according to Ermann, new contractions are excited while the circle remains closed, by bending back the nerve upon itself so as to cause points of its length to touch each other which were not previously in contact. Ritter and other physiologists have observed that, during the gradual loss of irritability which takes place in parts separated from the body, all parts of the nerve do not fail in their irritability with the same rapidity, but that the decline advances by degrees from the cerebral extremity of the nerve along its branches.

Some nerves, which are distributed to muscles, are nevertheless incapable

of exciting muscular contractions under the influence of the galvanic stimulus, both poles of the circle being applied to the nerves themselves.—This is the case with the posterior roots of the spinal nerves, while the anterior are excessively susceptible of the galvanic stimulus. (See p. 643.) I have likewise shown by experiment that the same stimulus excites no motor action when applied to the gustatory branch of the fifth nerve. (See p. 650.) This extraordinary result may be explained in either of two ways: namely, by supposing that the motor roots alone have the vital endowment of causing the muscles to contract, or by admitting, what is probable, that the motor roots transmit impressions in the centrifugal direction only, the sensitive roots only in the centripetal direction.

The stimulus of galvanism excites in all the organs of sense different sensations, in each organ, namely, the sensation proper to it.—The peculiar taste produced by including the tongue in a galvanic circle is well known. When a piece of zinc is applied to the point of the tongue, and silver to its back part, an acid taste is produced, which is rather sharp or alkaline when the metals are reversed. The same result may be obtained by using only one metal and a moist substance as an excitor of electricity, as in the following experiment described by Volta. A pewter cup filled with soap and water, lime and water, or, still better, with a moderately strong ley, being held with one or both hands previously moistened with water, and the point of the tongue brought into contact with the fluid, the sensation of an acid taste is immediately perceived. Pfaff* remarks, with reference to this experiment, that it appears to prove that the taste excited by the action of galvanism on the tongue is not owing to the decomposition of the muriate of soda of the saliva, and the disengagement of the acid at the positive, and of the alkali at the negative pole; for here the tongue being brought into contact with an alkaline fluid, the saliva could not have become acid. In fact, the taste produced by galvanism is, like all sensations of taste, the result of the specific reaction of the gustatory nerve; a particular taste therefore is only an internal condition excited in the nerve, and not a property of the stimulus which produces it. It has not at present been much observed whether peculiar smells are produced by the application of galvanism to the organ of smell; Ritter,† however, has perceived them; and it is a known fact, that the electricity excited by friction gives rise to the smell of phosphorus.

In the eye, a feeble galvanic current excites the special sensation of the optic nerve, namely, the sensation of light. Ritter and Purkinje have shown how the sensations of colours are excited in the eye. The sensation of light in the eye thus produced is not a developement of the matter of light, but is merely the reaction of the optic nerve, which is susceptible of the sensations of light and colours only, not of pain. It is a particu-

* Loc. cit. p. 736. † Beiträge zur näheren Kenntniss des Galvanismus, p. 160.

lar state of the optic nerve, just as pleasant and painful sensations are particular states of the nerves of common sensation. This view of the nature of the appearances of light in the eye has been established by the experiments of Purkinje and myself, and is also adopted, we observe, by physical inquirers of the first rank, for example by Pfaff.

In the auditory nerve, electricity produces the sensation of sound. Volta states that, when the poles of a battery of forty pairs of plates were applied to his ears, he felt a shock in his head, and a few moments afterwards a hissing and pulsatory sound like that of a viscid substance boiling, which continued as long as the circle was closed.* Ritter relates that, on closing the galvanic circle when both his ears were included in it, he was sensible of the sound of G treble:  if but one ear was in the circuit, and the positive pole applied to it, the sound was lower than G; if the negative pole was applied to the ear, the sound was higher.

2. *Of the changes produced in the excitability of the nerves by stimuli.*

Thus far we have considered merely the reaction of the nervous forces under the influence of stimuli. We have now to investigate the changes which these forces themselves undergo. All stimuli, which, by producing changes in the peculiar matter of nerves, excite reaction of them, are also capable of modifying their state of excitability. Reaction is always attended with an expenditure of power; it is the result of the material change; and, the longer the excitement is continued, the greater is the change produced. During a normal state of life the excitation is never so great that, in consequence of the change induced, the faculty of manifesting vitality by sensation is injured. The daily changes in the system, consequent on the action of stimuli, are counterbalanced by the processes of nutrition. But if the action of the stimulus be more violent, a longer time is required for restoration to be effected, and the stimulus may act with such violence as to exhaust the whole vital force of the organ. We are daily made conscious of these laws in the exercise of our power of muscular motion, of the generative function, and of the mental faculties; they are also exemplified in the effects of the immediate application of stimuli to the nerves. If a nerve is submitted to the long-continued action of galvanism, the muscular contractions which are excited become more and more feeble until at length they cease, and some time elapses before they can be re-excited; the nervous power, in fact, must first have been restored by the contact of the blood. It is the same with sensations. The longer the eyes are fixed upon a coloured object, the less distinct becomes the colour, till at length it is lost and the object appears grey; the retina acted on by the stimulus of light becoming exhausted, and at last insensible. In all these cases the exhaustion of

* Philos. Transact. 1800. p. 427.

the nervous excitability is the effect of the previous excitement, and not of any peculiar action of the exciting influences. The irritability may, however, be exhausted immediately, without previous excitement, by a foreign agent acting at the cost of the organic combination, and destroying the nerve while it annihilates the nervous power. This is the effect, for instance, of the most violent degree of electric action, as in lightning; of mechanical pressure likewise, by which the nerve and its primitive fibres are crushed : such also is the action of chemical agents, which destroy the organic combinations of the nervous substance, and decompose it; for example, of the mineral acids, the metallic salts, and pure alcohol.

If this external influence acts on all the nerves of the body simultaneously, as is done by the electricity in lightning or in the discharge of a strong battery, or if the whole length of a nerve is extended and stretched, the irritability of the whole system or of the whole nerve is destroyed. If the influence be such as affects only one point of the nerve, —as a caustic substance, pressure, or contusion,—the nervous power is destroyed in this point only, and between it and the muscle the nerve is still susceptible of being excited to motor action.

Heat and cold, when their action is not carried beyond a certain degree of intensity, nor continued beyond a certain time, are stimulants; but if their action be more violent and long continued, they have a contrary effect.

Cold, which, like heat, is capable of exciting inflammation and gangrene, benumbs the limbs, or deprives them of sensation and motion. This action may be either local or general: the local action of heat, when it does not produce inflammation and mortification, appears to excite, and not to benumb; but the general long-continued influence of heat is also productive of exhaustion of the nervous functions.

In the case of some influences which destroy the nervous power, a transitory excitement seems to precede the destruction of the excitability; this is the case when a nerve is crushed, or when an alkali is applied to it. The same phenomena of excitement are still more evident in the effects of a great part of the substances called narcotics; the principal action of which appears to be the production of a change in the composition of the nerves, and, when very violent, the abolition of the nervous power.

A large class of substances have, in the state of solution, a specific influence on the nerves, destroying their power, although they have no particular chemical properties as tested by reagents, and have not a solvent action on organic compounds generally. These are the "alterantia nervina," or "narcotics." They all produce a change in the material composition of the nerves. Some—for example, opium and nux vomica—are in small doses stimulant, the depressing action being

less marked; but all, when given in large doses, immediately deaden the excitability by producing change in the nervous matter. That such a change, not recognizable by our senses, nor by chemical tests, is really produced in the nervous matter, is probable, and it is necessary to adopt the supposition: but the only sign which we have of it is the loss of nervous power; the nerve which is paralyzed by the narcotic — at least, when a watery solution of a mere narcotic, for instance, of opium, is used,—differs externally in no respect from a sound nerve.

Before investigating more closely the action of narcotics on the nerves, we will inquire whether there are not substances capable of producing exaltation of their quality of excitability.

1. *Renovating stimuli.*— Earlier experiments seemed to favour the conclusion that many substances have the property of increasing the nervous power, and they thus promised results of great importance to practical medicine.* But the more powerful action of galvanism, after the nerves have been moistened with solution of chlorine or alkaline solutions, does not prove that these fluids increase the excitability of the nerves, but merely that the galvanic action is stronger; and Pfaff† has shown that the majority of such substances act by forming part of the galvanic circle, and by increasing the energy of the galvanic stimulus; they act, therefore, though more powerfully, yet in the same manner as water, which as a conductor is necessary to galvanic action. Medicine has ceased to expect any benefit from medicinal substances in the way of strengthening the nervous energy; the pretended virtues of such remedies are displayed nowhere but in the treatises on Materia Medica.

There are stimulants, it is true, in abundance; but they can strengthen the nerves only by promoting the reproductive process of nutrition in them. The remarks on the action of stimulants generally at pages 57—59, have equal force in the case of stimulants of the nerves.

2. *Alterant stimuli.*—Such are the narcotics, which, while they stimulate, seem to produce a change of composition in the nervous matter. It is by virtue of the latter property that in small doses they are useful in cases of paralysis, where they either remove slight material changes in the nerves, or produce such a change as enables nature to effect the cure. A more violent action of the alterantia nervina, or narcotics, is immediately destructive.

The change produced in nerves by the immediate application to them of a poison, causing paralysis, is not preceded nor accompanied by any signs of excitement, such as muscular twitchings. The application to the nerves themselves, in a rabbit, frog, or toad, of a watery solution of opium, of strychnine, or of spirituous extract of

* See Von Humboldt's Versuche über die gereizte Muskel-und Nerven-faser.

† Nordisch. Archiv. Bd. i. p. 17.

nux vomica, has, in my experiments, never excited muscular contractions; and I doubt if a narcotic applied directly to a nerve ever excites contractions of muscles; it must, I believe, act through the medium of the spinal marrow and brain. Strychnine, applied in powder to the moist spinal cord of the frog, excites no twitchings of the muscles; it must first enter the circulation, and thence act on the spinal cord, which transmits the influence to the nerves. Hence, when an animal is poisoned with opium or strychnine, if the nerves of an extremity are divided, the spasms in that limb cease; and if a portion of the spinal cord of an animal is destroyed before poisoning it with the upas ticuti, or angustura, all the parts which received their nerves from that part of the cord are exempted from the convulsive muscular contractions which ensue. These experiments prove incontestably that the narcotics do not excite contractions of the muscles by their direct action on the nerves, but through the medium of the spinal cord and brain.

There is another question, however; it is, whether narcotic poisons cannot, by their own action on the nerves, exhaust the irritability of the latter by an influence analogous to that of chemical stimuli. This question has been incorrectly confounded with the former, and an error has been committed in giving the same answer to both.

The most usual mode of action of narcotic poisons, when they paralyze the sensitive and motor powers of the nerves, is by being absorbed into the blood; thence acting in the capillary vessels on the brain, spinal marrow, and nerves. Their second mode of action, which is less rapid and more circumscribed, is by destroying locally the nervous power.

Action of narcotic poisons through the medium of the blood.—It was formerly imagined that the general effects of the local application of narcotic poisons arose from the local injury being propagated through the nerves; and even very recently, although the incorrectness of this view was already known, it has been tacitly adopted by Dupuy and Brachet; for they have maintained that animals cannot be destroyed by poison introduced into the stomach, if the nervus vagus have been previously divided on both sides. No such result was obtained in the numerous experiments performed by M. Wernscheidt under my direction. (See page 246). And it is now proved that the symptoms produced by the poison are due to its having entered the blood by imbibition. The first facts in support of the correct theory we owe to Fontana,* who instituted experiments with the poisons of the viper, ticunas, and laurel-berries, and with opium; and found that these and similar poisons do not produce their general effects, except they enter the circulation, and that they exert only a local influence on the nerves. Sir B. Brodie divided all the nerves of the anterior extremity in the

* On poisons, &c.

axilla of a rabbit, and applied the worara poison to a wound of the foot of the same limb; the action of the poison was not prevented. He applied a strong ligature to the hind-leg of a rabbit, excluding only the principal nerves, and then inoculated the leg with the worara; but no poisonous effects were produced until he loosened the ligature, when they immediately ensued.* Wedemeyer† found that prussic acid, of which the action was so strong that it proved fatal within a second when introduced into the eye and other parts of the body, produced no sudden effect when applied immediately to the nerves. Emmert amputated the extremities of animals, leaving them connected with the trunk by the nerves only, and then introduced poison into the feet; no general effect resulted. He likewise applied the poison to the nervous trunks themselves, but without effect. C. Viborg‡ has applied almost a dram of concentrated prussic acid to the brain of a horse laid bare by means of the trephine, without the slightest symptoms of poisoning being produced.§ Hubbard|| has, it is true, seen prussic acid, applied to the nerves, act rapidly; but he himself confesses that, when he isolated the nerve by placing a card beneath it, the poison produced no effect. The experiments of Magendie, Delille, and Emmert, detailed at page 238, prove that the rapidity with which poisons find their way into the circulation by means of absorption and imbibition, is very great; and Emmert has shown that the application of a ligature to the aorta prevents the general effect of poison introduced into the veins. The action of the angustura poison, of the upas, and of prussic acid, in Emmert's experiments, took place, when most rapid, in from two to five seconds. The difficulties attending the explanation of so quick an action have been considered at page 245.

I have myself also performed some experiments with a view to determine whether poisons produce their general effects through the medium of the nerves. I laid bare the ischiadic nerve in toads, and removed all the flesh of the thigh, leaving the leg and thigh connected to the trunk by means of the bone and nerve only. I then immersed the leg in a solution of acetate of morphia, and in a concentrated solution of opium, and kept the animals thus for a considerable time. No general symptoms of narcotisation were produced; even at the end of many hours, the animals retained perfect power of motion and sensation in the rest of the body.

* Phil. Transact. 1811, p. 178; 1812, p. 107.

† Physiol. Untersuch. über das Nervensystem und die Respiration; Hannover, 1817, p. 234.—Consult also Emmert, Tübing. Blätter. 1811. Bd. ii. p. 88. Salzb. Medic. Zeitung. 1813. Bd. iii. p. 62. Meckel's Archiv. i. p. 176. Schnell, Diss. Sist. Historiam Veneni Upasantiar. Tübing. 1815.

‡ Act. Reg. Soc. Med. Hafn. 1821, p. 240.

§ See Lund, Vivisectionen, pp. 103. 104.

|| Philadelph. Journal, Aug. 1822.

All the foregoing experiments tend to prove that the rapid general action of local poisoning is not effected through the medium of the nerves; but that the poison enters the blood, and is with it distributed to all the organs of the body. It is likewise susceptible of proof that *the general symptoms of poisoning are principally owing to the action of the blood, impregnated with the deleterious substance, on the central organs of the nervous system.*

1. After death produced by poisoning, the nerves and muscles are found to retain their irritability for a considerable time.

2. Ligature of the arterial trunk of an extremity does not exempt the latter from participating in the general effects of a poison subsequently administered, of which the action produces muscular spasms.* Paralysis of the heart, which Wilson observed to be caused in frogs by the application of infusion of tobacco or opium, will not, as Lund remarks, account for the symptoms of general poisoning; for frogs live many hours after their heart is cut out. The lungs again are not the organs principally affected; for supplying artificial respiration does not save the animal. While, on the other hand, if, in an animal poisoned with opium, strychnine, upas, or angustura, the nerves of an extremity be divided, the spasms in that part cease; so, also, destruction of a portion of the spinal cord puts a stop to the convulsions in the parts, the nerves of which arise from that portion of the cord. Opium, and the poison of serpents, appear to affect the brain and spinal cord equally: strychnine and the various poisons of the genus strychnos, and the poison of angustura, act more especially on the spinal cord; for tetanus and paralysis are the principal symptoms, and they continue, as Backer has shown, after division of the cord, in the parts supplied by nerves which come off below the section, although division of the nerves themselves puts a stop to them. The convulsions of the whole body, consequent on poisoning with angustura, continue likewise when the brain is wholly removed; the convulsive twitches being seen even in the ears.

The following experiment which I have performed on frogs, and which on repetition affords the same results, is very instructive. Having divided all the vessels and muscles of the thigh, and separated them from the bone, leaving the nerve uninjured, I poisoned the frog with nux vomica. The irritability of the sound leg was lost much sooner than that of the leg of which the muscles and vessels had been divided. After the usual effects of narcotic poisoning in frogs — namely, the state of excitability in which a slight touch generally excites convulsions, — had ceased, the muscles of the calf of the injured leg still contracted on my touching any point of the surface of the body; the leg, therefore, which received no blood was sensible to the influence of the spinal cord much

* See Lund, Vivisectionen, p. 109.

longer than the other limb, the nerves and muscles of which had been exposed to the action of the poison circulating in the blood; so that it is going too far to maintain that the poisons act on the central parts of the nervous system only; they act likewise on the nerves through the medium of the circulation. The general effects produced by the action of the poison on the spinal cord are, first, convulsions, then paralysis; its action on the nerves gives rise to no convulsive muscular contractions, but gradually destroys the nervous excitability.*

Local action of narcotic poisons on the nerves.—Certain as it is that the general effects of poisoning depend on the absorption of the substance into the blood, nevertheless the local action of poisons on the nerves cannot be denied.

Humboldt, Wilson Philip, and Brodie have shown that tincture of opium and infusion of tobacco paralyze the heart. In Humboldt's experiment the action of the heart was first accelerated, and then ceased altogether; the accelerated action was perhaps owing to the effect of the spirit of the tincture.

The most obvious case of local paralysis of nerves by a narcotic poison is the dilatation of the pupil, and loss of contractile power of the iris, consequent on the application of a drop of solution of extractum belladonnæ. In this instance the poison reaches the iris, and the ciliary nerves which are distributed to it, by imbibition. It is evidently a local effect, and not in the slightest degree the result of absorption into the blood, for the pupil of the other eye is unaffected. The local application of opium and morphia by frictions is likewise said to produce marked local effects, without any striking general action being manifested. The effects of the poison of lead, in producing paralysis of the hands, are also well known. To place the local action of narcotic poisons on the nerves beyond doubt, I dissected out the ischiadic nerve in a frog for a considerable extent, and let it hang in a solution of acetate of morphia; after a little time I found that the end of the nerve had wholly lost its excitability. The same was the effect of immersing the muscles in solution of opium, as Humboldt had already shown. I dissected out the ischiadic nerve in toads, and left the leg connected to the body by this nerve only, which, together with the leg, I then immersed in a strong watery solution of opium; in a short time the nerves and muscles lost all susceptibility of the influence of galvanic or chemical stimuli.

The local influence of narcotic poisons on the nerves is therefore certain. We must now inquire whether this effect extends beyond the nerves and muscles immediately affected. I have instituted direct experiments which prove that the local action of narcotics on nerves which

* Compare Lund, op. cit. p. 112. Backer, Commentatio ad Quæstion. Physiol. Traject. ad Rhen. 1830. See also Starnius, in Müller's Archiv. 1837, p. 223.

are laid bare, and insulated by dissection from other parts, remains limited to the point of application.

1. In the first place, the paralysis of the ischiadic nerve, by its immersion in solution of acetate of morphia or opium, does not extend to the muscles of the leg and their nerves. A mechanical or galvanic stimulus excites no contractions of the muscles when applied to the upper extremity of the nerve; but it does when applied to the lower part of the nerve, or to the muscles themselves. *The narcotic action, therefore, is not propagated from the trunk of a nerve to its branches.*

2. *The narcotic action does not react from a particular point of a nerve on the brain.*—I have already related experiments in which the nerves of the lower extremity in toads had been deprived of all excitability by the action of narcotics, but in which the other parts of the body remained uninfluenced. Other observations, however, render it probable that a gradual reaction does take place; for, whenever the nervous power of a part is exhausted, as by inflammation and mortification, exhaustion of the nervous power of the whole system gradually ensues. Here we perceive an important difference in the action of different influences on the nervous system; for,

a. The stimuli, which excite a manifestation of the nervous force, act instantaneously through the whole length of the fibres which are irritated at any one point. Thus the contraction of the corresponding muscles takes place at the very moment that the stimulus affects the nervous fibres, at whatever point of their course from the muscle to the trunk of the nerve it is applied; sensation is excited with equal rapidity.

b. The action of influences, on the contrary, which exhaust the excitability or power of the nerve, extends from its original seat very gradually to the sound parts of the nerve, and general symptoms slowly follow.

Thus loss of sight in an eye is gradually followed by atrophy of the optic nerve, which is likewise an effect of atrophy of the optic thalamus. Tabes dorsalis extends from below upwards. A violent injury of individual nerves is succeeded by a morbid state of the whole spinal cord,—namely, by tetanus.

3. *Dependence of the nerves on the brain and spinal cord.*

It was known that, after the division of a nerve, the portion cut off from communication with the brain retains, for a certain time, its excitability; but the question how far the continuance of the connection with the brain and spinal marrow is necessary for the longer preservation of the irritability of the nerves, and whether the muscles retain their irritability when their nerves no longer communicate with the central parts of the nervous system, could not hitherto be answered with certainty, and had in-

deed been seldom mooted. Nysten* had asserted that the muscles of patients who died a short time after an apoplectic seizure preserved their irritability, and contracted under the influence of the galvanic stimulus, although the functions of the brain had been paralyzed. I had good reasons, however, for believing that in such cases the nerves retain their power only for a short time, losing it entirely after a longer interval; for, in experiments on the reproduction of the nervous tissue in a rabbit, I had once observed that the lower portion of the nervus ischiadicus, which I had divided some months previously, had lost all its excitability; and a similar fact had been before observed by Fowler. I have since performed, in conjunction with Dr. Sticker, new experiments,† which have completely confirmed that supposition. To prevent the regeneration of the nerves, and to withdraw more effectually the lower portion from the influence of the brain and spinal cord, a portion of the nerve (the ischiadic) was entirely removed. The experiments were made only on two rabbits and a dog; yet the results were so constant, that they are quite worthy of dependence.

Eleven weeks after the division of the nerve in the first rabbit, it was laid bare in its course between the biceps and semitendinosus muscles. Contrary to expectation, and to our mortification, the continuity of the nerve was found to be restored. It was divided anew below the cicatrix; and it is remarkable that, although the animal uttered a loud cry, the section excited no contraction of the muscles. The lower portion of the nerve was now exposed to the galvanic stimulus of a single pair of plates, was cut and pulled in every possible way, but not the slightest muscular contraction was excited.

For the sake of comparison, the nerve of the opposite side was divided, when the animal showed signs of suffering the most severe pain, and violent muscular spasms took place; and, after the division, very slight irritation of the nerve itself,—that is to say, of the lower portion of it,—or merely of the muscles, excited strong twitchings, even after death.

Ten weeks after the division of the nerve in the dog, the ends were found to be reunited. The experiment was performed exactly as in the rabbit, and the result as to the effect on the nerve was entirely similar,—it had lost all its excitability; but the muscles still contracted slightly when stimuli were applied directly to them: immediately after death, however, this remaining irritability was gone, while in the muscles of the opposite leg the strongest contractions could be excited.

Five weeks after the nerve had been divided in the second rabbit, we proceeded to examine its state, and were the more interested on account of the short time that had elapsed since its division. The ends were

* Récherches de Physiol. et de Chim. Pathol.

† See Dr. Sticker's paper in Müller's Archiv. Bd. i. 1834.

not united; they were somewhat swollen, and connected with the surrounding cellular tissue. In the other instances, the portion of nerve removed measured about four lines only; here its length was eight lines. No contraction of the muscles could be excited by irritating the nerve either mechanically by a chemical stimulus—caustic potash, or by galvanism; nor by irritating the muscle itself, although the rabbit had plenty of vital power. On the left side the muscles were found irritable as in the other cases, both before and after death.

The foregoing experiments prove at least that, when the communication of the nerves with the brain is wholly cut off, they gradually lose the power of exciting the muscles to contraction, while the muscles lose their irritability. The result would, however, have been still more decisive if, in place of a single pair of plates, a small galvanic battery had been employed to stimulate the nerves and muscles. That, and that alone, would have enabled us to determine with certainty whether all the power of the muscles, in two of the cases, had been lost. The experiments as they were made, however, prove distinctly enough the necessity of communication with the brain for the preservation of nervous and muscular power. We may from them conclude also that if, after the division of a nerve, the excitability of the lower portion and the irritability of the muscles are restored, the nerve has itself been completely reproduced, and that this has not been the case if the nerve and muscle do not retain their vital properties.

CHAPTER III.

OF THE ACTIVE PRINCIPLE OF THE NERVES.*

The older physiologists had no determinate ideas regarding either the nature or the laws governing the actions of the nervous principle. They supposed that what they denominated "nervous spirits" were transmitted from the brain through the nerves and their ramifications to the different organs. When the actions of common electricity, and the modes in which it is conducted, became more fully known, physiologists imagined that the action of the nerves was rendered more intelligible by comparing them with electric apparatus. But it was not until the discovery of galvanism that the grounds of this and similar hypotheses were submitted to an exact inquiry.

Many observers, as Aldini, Galvani, Von Humboldt, Fowler, and others, were inclined to attribute the galvanic phenomena to an animal principle or force hitherto unknown; while Pfaff, Volta, and Monro, on the other hand, ascribed them to an electric agency developed by the action

* From J. Müller's article in the Encyclop. Wörterbuch der Medic. Wissensch.

of metals and moisture on each other, quite independently of the animal organs. Volta demonstrated the electric nature of this agency, and his view was in fine confirmed and placed beyond a doubt by the discovery that galvanic phenomena can be excited in other bodies without the aid or presence of animal substances. Monro likewise was at an early period of the inquiry led by his experiments to the correct conclusion that the galvanic fluid, which thus excites the action of the nerves, is electric in its nature, and altogether different from the nervous principle, acting merely as a stimulus of the nervous force, which then causes the muscles to contract.* Humboldt inferred, from several experiments which he performed, that the nerves are surrounded with a sensible atmosphere; his reason for that opinion was, that the galvanic influence transmitted through a divided nerve will pass from one portion to the other, even though the ends are not in contact. But we know now, that in such a case the interspace between the ends of the nerve is occupied by watery vapour, and that the circumstance adduced as a proof of the existence of a sensible atmosphere can be regarded only as an instance of the capability of gaseous exhalations to conduct the electric fluid. And here we perceive a marked distinction between electricity and the nervous principle: the action of the latter is interrupted by the ligature or division of a nerve; while, if the poles of a galvanic apparatus be applied to a divided nerve, or to one which is tied with a ligature, one pole above the point of division or seat of the ligature, the other below it, the electric fluid is transmitted as readily as before.

Although it is now certain that the phenomena produced in animals by galvanism are not due to an animal electricity, still many physiologists and men of science have not ceased to regard electricity and nervous power as principles in a certain degree similar; but a close inquiry shows that they are totally different. The experiments of Dr. Ure, and those of Dr. Wilson Philip, have among others given rise to misconceptions. In Dr. Ure's experiments, one of the wires connected with a galvanic battery of two hundred and seventy pairs of plates was applied to the spinal cord laid bare in the body of a criminal who had died by hanging an hour previously, while the other wire was applied to the ischiadic nerve. At the moment that the circle was closed, the muscles of the trunk were thrown into contraction as in a violent shudder. The motions of a laboured respiration, with the alternate rising and falling of the abdomen, were imitated by including between the wires the phrenic nerve and diaphragm, and alternately opening and closing the circle. In the same way horrid grimaces of the features were produced. But in all this there was nothing more extraordinary than in

* Monro's and Fowler's Abhandlungen über thierische Electricität. Leipzig, 1796. Fowler's experiments and observations relative to the influence called Animal Electricity. London, 1793.

the most common galvanic experiment, except that the human body was the subject of it. The experiments of Dr. Wilson Philip, in like manner, by no means justify the conclusions drawn from them. Even if it were a fact that a galvanic current, passed through the divided vagus nerve to the stomach, causes digestion to be performed in the same way as if effected by the influence of the nerve itself in the sound state, this would not prove the identity of the nervous principle and electricity; for the portion of a divided nerve, which is separated from the brain, retains for a certain time the power of exercising its ordinary functions when stimulated. Further, the repetition of Dr. Philip's experiments by Dr. Dieckhof and myself has not been attended with exactly the same results. (See page 550.)

The neurilema and the surrounding parts being moist, electricity would not remain insulated in the nerves, were it in action in them. It has indeed been imagined that the nerves have an insulating property. Fechner compares the nervous fibres to conducting wires covered with silk. But the neurilema itself is an excellent conductor of the galvanic fluid, and the nerves, as we shall show, have not a greater conducting power than other moist animal textures; for the galvanic current does not necessarily follow the ramifications of the nerves; it is only the nervous principle which takes that course. The galvanic current is conducted off from the nerves by the neighbouring tissues as readily as it is conducted by the nerves themselves, if a more direct course to the pole is thus afforded. The passage of the nervous principle again is interrupted by a ligature, while this has no effect on the transmission of the galvanic fluid.

Electricity is known by the bodies which insulate it, and which are conductors of it; these are its sole and certain tests, and in respect to them the nervous principle differs from it, and consequently cannot be identical with it. Other proofs, however, derived from properties of the nervous principle already alluded to, may be adduced:

1. When both poles of a galvanic battery are applied to a nerve, so that a galvanic current is transmitted through its thickness, the muscle to which it is distributed contracts, not because the galvanism reaches the muscle, but because the galvanic current passed transversely through the nerve affects it in the same way as mechanical violence, or the application of heat or caustic potash, and stimulates its motor power, the action of which is propagated only in the peripheral direction.

2. But if one pole is applied to the nerve, the other to the muscle, the galvanism does not fly transversely through the nerve, but from one pole to the other in a line from the nerve to the muscle; and the effect is the same as if both poles had been connected with the muscle. Here the excitability of the nerve is acted on in its whole course to the muscle.

3. If the nerve be bruised, or tied with a ligature, between the point

where both the wires are applied and the muscle, no contractions of the latter are excited. The galvanic fluid passes transversely through the nerve, as in the first case; but the action of the nervous principle is interrupted by the mechanical injury or ligature.

4. If, on the contrary, the poles be applied one above and the other below the injured spot or ligature, the galvanic fluid is conducted through it with perfect facility, and, stimulating the lower part of the nerve, gives rise to muscular contractions.

5. Nerves, even when perfectly dead, are still, like all moist animal textures, capable of conducting the galvanic fluid, though they have lost the power of exciting contractions in muscles.

6. Lastly, the experiments of myself and Dr. Sticker have shown that, when the vital influence of the nerves on the muscles has been interrupted for any considerable period, the stimulus of a simple galvanic circle is incapable of exciting their contraction. We found this to be the case in mammalia, in which we had several months previously divided the nerves in such a manner as to prevent their perfect reunion.

The discovery of electro-magnetism has furnished us with the most delicate galvanometers.

Vavasseur and Beraudi* have asserted that needles passed through the nerves of a living animal become magnetic, so as to attract iron filings. Division of the spinal cord, they say, deprives the nerves of the power of communicating to the needles the magnetic property, but the inhalation of oxygen restores it. The optic nerves do not communicate any magnetic power, even after the inhalation of oxygen. Nerves which were divided, or to which a ligature was applied, also lost the magnetizing influence; but still, at the distance of four lines between the divided ends of the nerve, a slight action on the needles was perceptible. I have taken the trouble to repeat these experiments on a rabbit, and have not been able to detect the slightest magnetic property in the needles which I employed.

M. David, in an inaugural thesis, published at Paris in 1830, detailed experiments of which the results were, that, when wires connected with a galvanometer were inserted into a nerve previously laid bare, an effect on the instrument was observable at the moment that the animal moved, while no motion of the galvanometer was perceptible when the nerve had been cut off from its communication with the spinal cord. I have repeated these experiments without success, and believe M. David to have been deceived. M. Person likewise failed to detect any electricity in the nerves by means of a very delicate electrometer.

MM. Prevost and Dumas† have proposed a theory of muscular action as dependent on electricity. They suppose that the different nervous

* Annali Universali di Med. Maggio, 1829; and Froriep's Notiz. No. 538.

† Journal de Physiologie, t. iii.

fibres, running transversely across the muscular fasciculi, attract each other, and thus shorten the fasciculi of the muscles; an hypothesis which, *à priori,* appears very improbable, from its assuming the innumerable muscular fibres to be themselves passive. That the reciprocal attraction of the nerves in the muscles is due to electric action is a second hypothesis. To prove the presence of electric currents in the nerves, the wires of the galvanometer must not be applied to the nerves and muscles at the same time; for a chain of heterogeneous animal substances, such as nerve and muscle, with a metal, is sufficient to develope electricity. The wires must be applied to the nerve only; and if then it be observed that, during voluntary motions, the action of this nerve which is in connection with the brain causes oscillations of the needle of the galvanometer, it might be concluded that the nervous power transmitted from the brain is an electric current. But Prevost and Dumas confess that in such an experiment they have never observed a deviation of the needle; not the slightest effect which they could perceive was produced on the galvanometer when they connected the wires with the vagus nerve in healthy animals, or the ischiadic plexus in an animal labouring under tetanus, whether the two wires were applied to different parts of an uninjured nerve, or to the two ends of a divided nerve. Nor did they observe the slightest declination of a needle which was suspended by a silk-worm thread near the surface of a muscle and nerve while in action; this I can confirm from my own observation. To explain the insensibility of the galvanometer to the action of the nerves, and to remove this main objection to their hypothesis, Prevost and Dumas avail themselves of another supposition; namely, that there are two galvanic currents in the nerves, which neutralize each other, and hence do not act on the galvanometer. They compare these supposed streams to the electric currents which traverse in opposite directions the arms of the galvanometer, and meet in the multiplier or coils of the conducting wires. The magnetic needle of the galvanometer represents the muscle, which in like manner experiences the action of the opposed currents. But in the galvanometer the needle indicates the presence of the opposed currents; why does it not indicate the presence of these imaginary currents in the nerves?

The attempt of the same celebrated physiologists to prove that the action of mechanical and chemical stimuli, and of great heat, on the nerves, depends on electric influence, demands particular attention; since a principal argument against the hypothesis of the electric action of the nerves is founded on the circumstance that all stimuli alike, and not merely electricity, are capable of exciting their active properties. To show that the action of fire on the nerves excites muscular contractions by an electric influence, they fixed two similar platinum wires

to the extremities of the conductors of the galvanometer, inserted one into the muscles of a frog, and with the other, which they had heated to redness, touched the nerves; muscular twitchings were excited, while at the same time a deviation of the needle of the galvanometer took place. This experiment, however, does not prove what the experimentor supposed; for portions of the same metal, of different temperatures, develope electricity as well as portions of different metals; there would therefore necessarily be a deviation of the needle produced in the experiment here described.

Prevost and Dumas endeavour further to show that chemical stimuli produce their effects on the nerves by developing electricity. They fixed to one of the wires of the galvanometer a piece of platinum, moistened with muriate of antimony, or with nitric acid, and connected the other wire with a portion of nerve, muscle, or brain; a deviation of the needle was observed each time that the circle was closed. This experiment proves still less than the preceding, for here the general conditions necessary for the developement of electricity by substances of different chemical composition were present. The following experiment is similar: to the two conductors of the galvanometer, similar plates of platinum were fixed, and a portion of fresh muscular substance of several ounces' weight, taken from a living animal, was connected with one of them: the two conductors were now immersed in blood, or in a weak saline solution, when a deviation of the needle took place.

The most recent experiments performed with the aid of the galvanometer are those of M. Person,* who, although the action of his instrument was most delicate, failed, like Prevost and Dumas, to detect electric currents in the nerves. M. Person connected the conductors of the galvanometer with the anterior and posterior parts of the spinal cord in rabbits and in kittens; he inserted them into the interior of several thick nerves; he repeated these experiments after having injected tincture of nux vomica into the abdomen so as to produce spasmodic action of the muscles; but he in no instance observed distinct evidence of electric action. He relates a circumstance which shows how suspicious we ought to be lest accidental occurrences mislead us in researches of this kind. One day, having placed a drop of water on zinc to ascertain that the galvanometer acted well, and having observed a deviation of the needle on touching the zinc and water with the wires of the galvanometer, he connected the platinum wires with the spinal cord of a young dog, and perceived a deviation of the needle to the extent of from thirty to forty centimeters; but the deviation took the opposite direction when the wires were reversed, which led to the suspicion that one of the wires was the seat of an electro-chemical action. And such proved to be the case: for, on immersing the wires in blood or water,

* Sur l'hypothèse des Courans Electrics dans les Nerfs. Journ. de Physiol. t. x. 1830.

while with one he touched a piece of zinc, Person found that the zinc became oxidised by the galvanic current which was excited.

To the experiments with the galvanometer it might be objected that this instrument is capable of indicating the presence of continuous currents only, while the contractions of muscles are intermittent actions. Person found, in fact, that when one of the wires of the galvanometer was connected with the conductor of an electrical machine, and the other made to communicate with the earth, a regular deviation of the needle took place "à chaque tour du plateau," which was not the case when the electricity, instead of being emitted in a stream, was elicited in a series of sparks. Person subsequently repeated several of his experiments with an instrument which was affected by interrupted currents (courans instantanés); but even with this instrument he could observe no sign of the developement of electricity during muscular contractions. M. Person remarks lastly, that, to excite contractions of the muscles, it is not necessary that the galvanic current pass the whole length of the nerve; that, if transmitted transversely through it, it acts equally well; that in this case it cannot be supposed to be diverted along the whole course of the nerve, for a nerve is not a better conductor of electricity than other moist animal substances. From the experiments of Person, as well as from all the facts stated in this chapter, we must conclude that a motor nerve during life, and while it retains its irritability, is in such a condition that every cause which produces a sudden change in the relation of its molecules to each other, whether it be an electric, chemical, or mechanical stimulus, excites a muscular contraction at the peripheral extremity of the nervous fibres. The experiments instituted with the galvanometer certainly afford no proof of the existence of electricity in the nerves, but they by no means prove its absence; the instruments are too imperfect. They do not give evidence of the presence of the electricity developed by a pair of metallic plates when the connection of one of the conductors of the galvanometer with the metal is rendered mediate only, for instance, by the interposition of a drop of water or piece of muscle. Hence we perceive distinctly, that, even if electricity were an active principle in the nerves, it would not be easy to detect it by means of the galvanometer. The nerve of the frog's leg, however, which is a much more delicate electrometer, is not at all influenced by contact with another nerve at the time subjected to irritation.

The electric fishes have been adduced by some physiologists in support of the hypothesis of the electric action of nerves: but the very fact of the existence in these fishes of organs constituted after the manner of galvanic piles (see page 65), is unfavourable to the theory, for if electricity were an active principle of the nerves, the fishes would require only conductors, and not a special galvanic apparatus. The anecdote is frequently related of Cotugno having felt a violent shock when the

tail of a mouse, which he was dissecting alive, struck his hand; but this circumstance had nothing to do with electricity; for when animals, such as mice, frogs, or spiders, towards which we are apt to feel repugnance, are held in the hand, a slight cause is sufficient to excite nervous symptoms, quite independent of electricity. The sensation produced by an electric shock is not peculiar to that agent; it may be produced by any strong excitement of the nerves, whether mechanical or mental. Kastner relates that in writing he frequently sustains slight shocks in the fingers. Some years ago, when I was labouring under a state of nervous excitability, I had this sensation very frequently on using the hand and fingers much.

The conclusions which must be drawn from the preceding considerations are:—1. That the vital actions of the nerves are not attended with the developement of any galvanic currents which our instruments can detect. 2. That the laws of action of the nervous principle are totally different from those of electricity. 3. To speak, therefore, of an electric current in the nerves, is to use quite as symbolical an expression as if we compared the action of the nervous principle with light or magnetism. Of the nature of the nervous principle we are as ignorant as of the nature of light and electricity; but with its properties we are nearly as well acquainted as with those of light and other imponderable agents. However much these various principles differ from each other, the same question applies to all, namely: are their effects produced by currents of an imponderable matter travelling through space, or by the undulations of a fluid? which theory be correct in the case of the nervous principle, is at present a matter not affecting the study of the laws of its action; just as the laws of optics must remain the same, whichever theory of the nature of light be adopted.

SECTION II.

Of the nerves of sensation, the nerves of motion, and the organic nerves.

CHAPTER I.

OF THE SENSITIVE AND MOTOR ROOTS OF THE SPINAL NERVES.*

THE fact that the same nerves supply the body with sensitive and motor power, and that one of these functions of a nerve may in consequence of paralysis be lost while the other is preserved, is one of the most important in Physiology. Sir Charles Bell first conceived the ingenious idea that the posterior roots of the spinal nerves, which have upon them a ganglion, are the source of sensation; the anterior roots, of motion; and that the primitive fibres of these roots after their union are mixed, and thus distributed for the supply of the skin and muscles. This view he proposed in 1811, in a treatise entitled, "An idea of a new

* Principally derived from the papers of J. Müller in Froriep's Not. Nos. 646 and 647, and in the Annal. des Sc. Nat. 1831.

anatomy of the brain, submitted for the observation of the author's friends." Eleven years later the same theory was advanced by M. Magendie, who, however, has the merit of having first subjected it to the test of experiment in the case of the spinal nerves. M. Magendie maintained as the result of his experiments that division of the posterior roots of the nerves deprived the corresponding parts of the body of sensation only, while division of the anterior roots deprived them of motion. M. Magendie's results were only approximative. He asserted that the posterior columns of the spinal cord, and the posterior roots of the nerves, supplied sensation principally; the anterior principally motion; but that the latter were not wholly devoid of sensitive power. Thus, in his experiments, the application of galvanism to the posterior roots of the spinal nerves after their separation from the spinal cord excited contractions of the muscles, though these were but feeble; while the same stimulus applied to the anterior roots gave rise to violent muscular spasms.* These experiments, performed on the higher animals, are the most cruel that can be imagined. The extensive wound necessary for laying open the spine in sufficient length to enable the operator to divide the roots of all the nerves which go to the posterior extremities, produces a great shock to the system, is attended with very great hemorrhage, and death inevitably follows in a short time, before satisfactory results can be attained. Great, therefore, as was the interest which Sir C. Bell's theory, thus newly illustrated by M. Magendie's experiments, excited, a satisfactory confirmation of the results was still wanting. Béclard was the only physiologist who spoke on the point in a decided tone, but it was at the same time in too superficial and unconvincing a manner: he says,† "Les expériences de M. Ch. Bell, celles de M. Magendie, et les miennes propres, ont clairement démontré que la racine postérieure des nerfs spinaux est sensoriale, et la racine antérieure motrice." Fodéra's experiments were accompanied with such contradictory symptoms that it is inconceivable how he could put them forth as confirmatory of M. Magendie's observations. Bellingeri obtained totally different results, and arrived at the conclusion that the internal grey substance of the spinal cord supplies sensation; the white fibrous substance, the motor power; that the anterior columns and the anterior roots are destined for the motions of flexion, and the posterior for those of extension. The above experiments were carefully repeated in Germany by M. Schoeps on many animals;‡ but the results obtained were very doubtful and uncertain. I had myself, as early as 1824, during my stay in Berlin, performed them without success. More recently, being engaged in researches

* J. de Physiol. ii. 276. Compare Desmoulins et Magendie, Anat. et Physiol. des Systèmes Nerveux. Paris, 1825. p. 777.

† Elém. d'Anat. Générale. Paris. 1823, p, 668.

‡ Meckel's Archiv. für Anat. u. Physiol. 1827.

on the nervous system, the desire of ascertaining the real facts of the case induced me to perform a new series of experiments on rabbits, and on a different plan. The mode in which the investigation had previously been conducted is evidently deceptive, from the circumstance that many animals, especially rabbits, are so much frightened by the first steps of the experiment, before they have suffered any considerable injury, that the most violent irritation of the skin, not even pinching and cutting it, causes them to manifest any pain. How then can we, in the short time which an animal lives after the spinal canal is opened, determine with certainty whether it has sensation or not?

I knew that the slightest stretching of a nerve, when tense, with a needle, excites contractions in the muscles to which it is distributed. If then the posterior roots of the spinal nerves are merely sensitive, and not endued with motor power, they ought, when irritated with the needle, to excite no contractions of the muscles; while these ought to ensue from irritation of the anterior roots: that I might perceive the most trifling twitchings, I laid bare the muscles of the posterior extremities. Experiments thus performed, I repeated several times, but I must confess without obtaining any certain result, since the shocks produced in opening the spinal column had given rise to tremors of the muscles which rendered the results of the further part of the experiment unsatisfactory. After so many unsuccessful attempts to verify M. Magendie's assertion, I began to doubt the possibility of obtaining a decided and satisfactory result from all such experiments. Desmoulins and Magendie themselves, however, have merely said, that, in the one case, *nearly all sensation*, in the other, *nearly all power of motion*, is lost. In deciding a question absolutely, no half results, no approximatives, are sufficient. The theory of Bell was extremely ingenious, but its truth appeared to me still to require demonstration; even Magendie had not decided it satisfactorily. I thought it perhaps impossible to decide it with certainty in the higher animals. This opinion, that the theory of Bell had not been properly established by experiment, was held by Prof. E. H. Weber also.*

The happy thought at length occurred to me of performing the experiment on frogs. These animals are very tenacious of life, and long survive the opening of the vertebral canal. In them, also, the nerves retain their excitability for a very considerable time, and the large roots of the nerves of the posterior extremities run a long distance within the cavity of the spine before uniting. The result was most satisfactory. The experiments are so easily performed, so certain and conclusive, that every one can now very readily convince himself of one of the most important truths of physiology.

* See page 283 of his excellent translation of Hildebrandt's Anatomie.

To lay open the spine, I make use of a small pair of bone-nippers, which cut sharply at the edge and points. The operation is completed in a few minutes, without any injury to the spinal cord. The frogs remain quite lively, and leap about as before. As soon as the spinal canal and the membranes are laid open, the thick posterior roots of the nerves, given off to the lower extremities, come to view. They should be carefully raised with a cataract needle, without including any of the anterior roots, and cut off close to the spinal cord. The end of one of the posterior roots is now seized with a pair of forceps, and the root itself irritated repeatedly with the point of the needle; but not the slightest contraction of the muscles of the posterior extremities ever ensues. The same experiment may be repeated on the very large posterior roots of the nerves of the anterior extremities, and the same result will be obtained.

If, now, one of the anterior roots of the nerves of the lower extremity, which are equally as large as the posterior, is raised with the needle out of the vertebral canal, it is found that the slightest touch of these anterior roots excites the most powerful contractions of the whole limb. Having cut them through at their insertion into the cord, the extremity of one is seized with the forceps, and the needle used to irritate it as in the case of the posterior root; and, each time that the point of the needle is applied, most distinct twitchings of the muscles take place.

These experiments may be repeated on a large number of frogs, and they will most convincingly prove that *it is quite impossible to excite muscular contractions in frogs by irritating mechanically the posterior roots of the spinal nerves; and that, on the other hand, the slightest irritation of the anterior roots immediately gives rise to very strong actions of the muscles.*

As long as both roots of the nerves are in connection with the spinal cord, the traction experienced by the cord itself, when the posterior roots are raised, may cause the production of muscular twitches in the limbs; such effects, however, are quite independent of the action of the posterior roots, and depend solely on the irritation communicated to the anterior roots by the spinal cord in consequence of the mechanical violence which this has suffered. Hence, if the latter roots have been previously divided, no mechanical irritation of the spinal cord itself, or of the posterior roots connected with it, excites the slightest muscular contractions.

The experiments with the galvanic stimulus of a single pair of zinc and copper plates are equally conclusive.

The application of galvanism to the anterior roots of the spinal nerves after their connection with the cord is divided excites violent muscular twitchings; the same stimulus applied to the posterior roots is attended with no such effect. This result is very remarkable, and is what I did

not at all expect: for I imagined that, although the posterior roots are endowed with sensation merely, they might still conduct the galvanic fluid to the muscles; and when a powerful galvanic pile is employed this is inevitably the case (as in Magendie's experiments), the strong galvanic current being conducted by the posterior root of the nerve as by any animal substance; but the stimulus of a single pair of plates, while it causes the anterior roots of the nerves to give rise to muscular contractions, has no such influence when applied to the posterior roots. In this experiment it is necessary to be very cautious that the plates are brought into contact with no other parts than the nerves.

The experiments may be performed on frogs in the manner adopted by Sir C. Bell and M. Magendie, and the results are as certain as in those just detailed. If in the same frog the three posterior roots of the nerves going to the hinder extremity be divided on the left side, and the three anterior roots on the right side, the left extremity will be deprived of sensation, the right of motion. If the foot of the right leg, which is still endowed with sensation but not with the power of motion, be cut off, the frog gives evidence of feeling pain by movements of all parts of the body except the right leg itself, in which he feels the pain. If, on the contrary, the foot of the left leg, which has the power of motion but is deprived of sensation, is cut off, the frog does not feel it. This experiment is the most striking of all, and the result is decisive; because, on account of the small number and large size of the roots of the nerves going to the posterior extremity in the frog, we can be certain that all are divided.

The foregoing experiments leave no doubt as to the correctness of Sir C. Bell's theory.

I may further remark that the section of the posterior roots, in dividing them from the spinal cord, is frequently attended with very distinct manifestations in the anterior part of the body that pain is suffered.

In the experiments hitherto detailed, both poles of the galvanic apparatus were applied to the roots of the nerves; a galvanic current, therefore, was transmitted transversely through them: I was anxious now to know (and the question will occur to every one) whether the posterior roots, being incapable of exciting muscular contractions when themselves irritated, are also non-conductors of the galvanic fluid, and do not convey it to the muscles when one pole is connected with them, and one with the posterior roots of the nerves. This gave rise to the performance of a series of interesting experiments on frogs, which I have since frequently repeated, and which afforded constantly the following results: namely, that the posterior root of the nerve does conduct a galvanic current, but that the twitchings excited occur only in those muscles which lie within the galvanic circle; while, when the galvanic

stimulus is applied to the motor roots, whether both poles be connected with them, or one with them and the other with the muscles, contractions are excited in all the muscles of the extremity, not merely in those which lie within the galvanic circle, but in all down to the very toes; and the same takes place when one pole is connected with the posterior, the other with the anterior roots of the nerves. In these experiments a plate of glass was always inserted beneath the nerves to which the galvanism was applied, and the frog was also laid upon a piece of glass.

The foregoing experiments prove as satisfactorily as is possible:

a. That the posterior roots of the spinal nerves have not an insulating action on the galvanic fluid; but are, like all moist animal textures, passive conductors of it, transmitting it from one pole to the other.

b. Although (as the first detailed experiments showed) they have no motor power, and can themselves excite no muscle to action.

c. That, on the contrary, the anterior roots are not mere conductors of the galvanic fluid; but that the direct action on them of any stimulus, whether mechanical or galvanic, excites in them a motor force (different from galvanism), the action of which extends through all their branches.

I have already shown (page 621) that a nerve may lose its special motor power without ceasing to be a conductor of the galvanic fluid.

To give the experiments which I have detailed a still greater interest, I determined to repeat them; using, instead of a single pair of plates, a galvanic pile of thirty-four pairs of plates of somewhat more than four inches square. They were performed on frogs, and the results were constantly the same as in the former experiments.

To ascertain whether the roots of the last spinal nerves are capable, when irritated, of exciting muscular contractions in the anterior parts of the body,—for example, in the head through the medium of the spinal cord,—I applied the poles of the galvanic apparatus to the stumps left, when the roots of those nerves had been divided at some little distance from their origin. The results were constant, but unexpected: no contractions of the anterior parts of the body were excited, either when the wires were applied to the anterior or to the posterior roots. It appears, therefore, that the fibres of the nerves do not communicate in the spinal cord. Muscular contractions were excited, however, when one pole was applied to the roots of the nerves, and the other to the exposed textures of the anterior parts of the body; in which case the galvanic current itself was conducted to distant motor nerves.*

* I have every year in my lectures repeated the experiments on the sensitive and motor roots of the nerves, with mechanical irritation and the galvanic stimulus of a single pair of plates; I have performed them also in the presence of MM. Humboldt, Dutrochet, Valenciennes, Laurillard, Cuvier, Tiedemann, Weber, Wutzer, and Retzius, and always with the same satisfactory results. They have been repeated with

The difference with regard to motor and sensitive properties, which has been established so clearly in the case of the anterior and posterior roots of the nerves, has not been by any means demonstrated to exist between the anterior and posterior columns of the spinal cord. (See the 2nd chapter of the 5th section of this Book.)

CHAPTER II.

OF THE SENSITIVE AND MOTOR PROPERTIES OF THE CEREBRAL NERVES.

We shall not here enter in detail into the subject of the physiology of the individual cerebral nerves, but merely inquire how far they agree with or differ from the spinal nerves.

The cerebral nerves may be arranged in the following classes:—

1. *The nerves of special sense:* the olfactory, optic, and auditory nerves.

2. *Mixed nerves with double roots:* the nervus trigeminus, nervus glosso-pharyngeus, (see page 609), the nervus vagus cum accessorio, and, in several mammalia, the nervus hypoglossus (see page 609).

3. *Single-rooted nerves, for the most part of motor function, which are either themselves entirely motor, and receive sensitive fibres from other nerves, or which, if their roots contain sensitive fibres, still cannot be classed with the double-rooted spinal nerves.* These are the nervus oculo-motorius, the trochlearis, the abducens, and the facial nerve.

The nerves of the last two classes require a particular consideration.

Mixed cerebral nerves with double roots.

Nervus trigeminus.—The two roots of this nerve, the portio major which expands to form the ganglion Gasseri, and the portio minor which has no ganglion, and passes under the ganglion of the portio major to join the third branch which issues from it, are well known. The first and second divisions of the nerve, which arise wholly from the ganglion of the portio major, are probably purely sensitive. The third division, which is formed in part by the portio minor, and receives another portion of its fibres from the Gasserian ganglion, is both motor and sensitive.

Of the branches of the first division of the nervus trigeminus, the nasal is known to be a nerve of sensation, from its distribution principally to the nose, to the inner angle of the eye, to the conjunctiva and lachrymal sac. The frontal nerve might be supposed to be a motor

success by Dr. Thomson, in Edinburgh, and by Dr. Stannius, in Berlin. (See Hecker's Annal. Dec. 1832.) Seubert (De funct. rad. ant. et post. nerv. spin. Carlsruhæ, 1833,) and Van Deen (De different. et nexu inter nervos vitæ animalis et organicæ; Lugd. Bat. 1834,) obtained the same result from mechanical irritation of the two roots. But Seubert failed with galvanism, because he used too powerful a battery. Panizza's experiments, likewise, on frogs and goats confirm the truth of Bell's theory. (Panizza, Richerche sperimentali sopra i nervi. Pavia, 4.)

nerve, since it is described as ramifying, not merely in the skin of the forehead and upper eyelid, but also in the orbicularis palpebrarum, occipito-frontalis, and corrugator supercilii muscles. But there are also branches of the facial nerve distributed to these same muscles; and Sir Charles Bell has shown that the frontal nerve is probably endowed with sensation only, and that the parts just mentioned receive their motor nerves from the facial. Sir C. Bell divided the frontal nerve in a man suffering under neuralgia. The section of the nerve was attended with great pain. In another patient, the superior portion of the facial nerve was destroyed by an ulcer in front of the ear, and paralysis of the corrugator supercilii was the consequence. More recently, Sir C. Bell has observed two or three cases of disease of the ophthalmic nerve, in which there was total insensibility of the eye and eyelids, without loss of vision.

The second division of the fifth nerve is also a nerve of sensation merely, and may be satisfactorily shown to contain no motor fibres. Several of its branches, as the anterior and posterior dental nerves, the vidian, nasal, palatine, and naso-palatine, are known by their distribution to be merely sensitive nerves. The subcutaneus malæ and infra-orbital branches may be inferred to be nerves of sensation, from their distribution in greater part to the skin; and the infra-orbital, which forms many anastomoses with the facial nerve, and is transmitted through, rather than distributed to, the muscles of the face, can be distinctly proved to have no motor fibres.*

Sir C. Bell divided in animals the infra-orbital nerve on the left side, and the facial nerve on the right side of the face; the result was complete insensibility of the left side, and loss of motion on the right side. The division of the facial nerve excited contractions of the muscles of the face, that of the infra-orbital nerve did not. The same physiologist divided in one ass the infra-orbital nerve; in another, the facial. In the last, the power of motion was lost, sensibility retained; in the first, the reverse was the case. He irritated mechanically the infra-orbital nerve in an ass; violent pain was produced, but no twitchings of the muscles. These experiments have been verified by Schoeps† and myself.‡ Sir C. Bell has related a case in which a man, in consequence of injury of the infra-orbital nerve, lost sensation in the upper lip, the power of motion being preserved. He is in error, however, in supposing that the motion of the upper lip of animals, in grasping food, depends on the infra-orbital nerve. He states that, after he had divided that nerve on both

* See Sir C. Bell's Natural System of the Nerves, and his papers in the Transactions of the Royal Society for 1821, 1823, and 1826; Magendie's Journal, tom. ii. p. 66; Eschricht, De function. nervorum faciei et olfactus organi. Hafn. 1825; and Backer, Commentatio ad quæst. physiol. à facult. Med. Acad. Rhenotraj. a. 1828. proposit. ad Rhen. 1830. † Meckel's Archiv. 1827, p. 409. ‡ Froriep's Notiz. No. 647.

sides, the ass no longer seized the food with its lips, but merely pressed them against the ground, and used the tongue for the prehension of the food. Both Sir C. Bell and Schoeps remark also, that, when the facial nerve had been cut through on one side, the animal still moved its lips on both sides in seizing its food. Mr. Mayo* first corrected this error. He found that, after the infra-orbital nerve had been divided, the animal did not seize its food with the lip, and could not use it well during mastication; but it could open the lips, which Sir C. Bell had denied. The phenomena in Sir C. Bell's experiments were justly attributed by Mr. Mayo to the loss of sensation in the lips; the animal not being able to feel the food, although it had the power to seize it. Mr. Mayo has, on the other hand, proved incontestably that the lips receive their motor power from the facial nerve; for, by dividing the facial nerves on both sides, he produced paralysis of all the muscles of the face, and of the lips also. The motion of the lips on both sides, when the facial nerve has been divided on one side, is explained by M. Backer, and correctly, as depending on the passive motion of the paralysed with the other side during the contraction of the orbicularis oris.

I have myself instituted the following experiments with reference to the properties of the infra-orbital nerve in rabbits. However much I irritated the nerve with a needle, pulled it, or pinched it with forceps, I could excite no twitchings of the muscles. I divided the nerve close to its exit from the bone; the animal uttered a cry of complaint, and gave signs of suffering very great pain. The nerve was laid upon a piece of glass, and its extremity was included in the galvanic circle of a pair of metallic plates; not the slightest contractions were observed in the muscles of the nostrils, which were laid bare. Twitchings of the muscles ensued, however, when one of the plates was connected with the nerve, the other with the muscles; but a galvanic current was thus transmitted directly to the muscles themselves, and excited contractions of them quite independently of the infra-orbital nerve. We then connected with the insulated extremity of the nerve the poles of a galvanic pile of sixty-five pairs of plates; the nerve was very broad, and, when some points of it were touched, no muscular contractions were excited, while the contact of the wires with other points of the nerve gave rise to slight twitchings of the snout, which was an unexpected result, to be explained in two ways: 1st, by supposing that branches of the facial nerve join the infra-orbital immediately at its exit from the bone; or 2ndly, by supposing that, when a very powerful galvanic battery is used, the galvanic current not only takes the most direct course, as usual, from the one pole to the other, but is also led off in other courses by all conducting bodies. That there is some ground for the last supposition

* Anat. and Physiol. Comment. p. 107.

is shown by the fact that, although a stimulus applied to a nerve does not cause it to excite contractions of the muscles to which it is distributed, if the nerve be bruised below the point to which the stimulus is applied; yet if a very powerful galvanic battery, namely, of eighty or one hundred pairs of plates, be employed, and both poles applied above the bruised portion, the galvanism acts on the lower portion of the nerves, and excites its motor power.

The experiments of Sir C. Bell, M. Schoeps, Mr. Mayo, and myself, prove, therefore, that all the branches of the first and second divisions of the nervus trigeminus are nerves of sensation, and not of motion.

The third division is evidently both sensitive and motor, like the spinal nerves, which are likewise composed of a root provided with a ganglion, and another on which no ganglion is formed. Its function is shown by its distribution. This third division of the fifth, rather than the whole nerve itself, is analogous to the spinal nerves.

The masseteric, deep temporal, buccinator, pterygoid, and mylo-hyoid branches, those given to the levator and tensor palati muscles, and the nerve of the tensor tympani, which arise either immediately or mediately from the third division of the fifth, are evidently motor. But the fact of the masseteric giving branches to the maxillary articulation shows that they contain sensitive fibres likewise.

The inferior and posterior portion of the third division of the fifth nerve is, on the other hand, composed wholly of sensitive fibres. The nervus auricularis seu temporalis superficialis is not distributed to muscles; it unites with the facial nerve, as well with the trunk of that nerve as with its branches, and imparts to it a part of the sensitive power which it (the facial nerve) possesses, in addition to its motor faculty. The ramus auricularis is distributed to sensitive parts merely; namely, to the meatus auditorius externus, to the external ear, and the skin of the head. The mylo-hyoid is not a branch of the inferior dental nerve; these two nerves have, as Bell remarks, no further connection, than that they run parallel with each other, side by side, till they reach the foramen dentale. The dental nerve itself is evidently intended merely to endue the parts it supplies with sensation. That the branch which issues from the mental foramen is a nerve of sensation, is proved by the case observed by Sir C. Bell, in which it was injured in the extraction of a tooth, and the lower lip in consequence rendered insensible. It can likewise be proved very satisfactorily that the gustatory branch, although it is distributed to the muscular substance of the tongue, is a sensitive nerve, and has no motor power.

Desmoulins had made the remark that, if the gustatory nerve is stretched in a dog, the animal utters a cry, the tongue remaining motionless; and that the application of galvanism to the nerve after death causes no motion of the tongue. This last experiment I have

instituted* on rabbits during life; the nerve being divided, and then irritated with a needle, or with the stimulus of a battery of sixty-five pairs of plates: the result was as Desmoulins states. Magendie also has observed that division of the gustatory nerve is followed by loss of sensation, without loss of motion in the tongue. I have satisfied myself that this nerve is capable of the sensation of pain, and it will be shown at a future page that it is also the nerve of taste.

From the facts which we have stated, it results that the fifth nerve, by virtue of its greater root, supplies all the anterior and antero-lateral parts of the head with common sensation, there being other nerves for the special senses of smell, sight, and hearing; and that, by virtue of its smaller root, it is the motor nerve of all the muscles engaged in mastication. Hence, in Magendie's experiments, the division of the trunk of the nerve put a stop to all the movements of mastication, and deprived the whole anterior part of the head, the eye, nose, and tongue, of common sensibility; and disease of the trunk of the nerve, or of its roots, has been observed by Bell, Magendie, and Serres, to be attended with the same results. The result of division of the nerve within the cavity of the cranium, an experiment performed by Magendie and repeated by Eschricht, was loss of sensibility of the entire side of the head. The mucous membrane of the nose, as well as the conjunctiva, were rendered insensible to puncture, and to chemical irritants, such as liquor ammoniæ. The eye was dry, the iris contracted, and the winking of the eyelid was no longer observed. On the following day, the eye of the sound side was inflamed in consequence of the stimulus of the ammonia; the other eye was free from inflammation, the developement of which, therefore, had been prevented by the want of sensibility. In other experiments, division of the nerve was followed, at the expiration of several days, by inflammation of the conjunctiva, secretion of purulent matter from the eyelids, iritis, and the formation of pseudo-membranes in the eye itself. Other effects are a softened unhealthy state of the gums; the tongue becomes white on the affected side, and its epithelium thickened.

Nervus glosso-pharyngeus.—I have shown at page 609 that this nerve also has two roots, one of which has a ganglion. Its distribution corresponds with this structure. It supplies the mucous membrane of the back part of the tongue, and it also gives branches to the pharyngeal muscles, particularly to the stylo-pharyngeus; and it is proved to have motor power by the observation of Mayo, which I have since repeated in a rabbit, that the application of galvanism to the nerve, even after death, excites muscular contractions in the pharnyx.

[It appears, however, from the experiments of Dr. J. Reid,† that the

* See Froriep's Notiz. No. 647.

† Experimental Investigation into the Functions of the Eighth pair of Nerves, in the Edinb. Med. and Surg. Journ. for Jan. 1838.

conclusion deduced from Mr. Mayo's experiment is erroneous, and that the glosso-pharyngeal nerve is really a nerve of sensation only. The experiments performed by Dr. Reid on this nerve were twenty-seven in number; the subjects of them were dogs; Dr. Alison and Professor Sharpey were in many instances present, and confirmed the observations. The results afforded were the following: 1. The glosso-pharyngeal nerve is a nerve of sensation; distinct indications of suffering were given when the nerve, particularly its pharyngeal branches, were irritated or pinched in living animals. 2. Mechanical or chemical irritation of the nerve, before it has given off its pharyngeal branches, or of any of these branches, gives rise to extensive muscular motions of the throat and lower part of the face; but these motions are also excited by irritating the upper or cranial end of the cut nerve before it has given off any of its branches, while irritation of the lower end, or that in connection with the muscles, is followed by no movement (Exp. VII.); so that these motions must depend on an influence transmitted to the muscles through other nerves by the intervention of the central organs of the nervous system. 3. Lastly, when the functions of these central organs have been arrested by poisoning the animal with prussic acid, irritation of the glosso-pharyngeal nerve, before it is joined by any communicating twigs from the pharyngeal branch of the vagus, gives rise to no movements in the muscles to which it is distributed, namely, the constrictor muscles of the pharynx, which were exposed to view; while, on irritating the pharyngeal branch of the par vagum, rapid and vigorous movements of all the pharyngeal muscles and upper part of the œsophagus follow. In most of the experiments from which this last result was deduced, the nerves were not cut off from their connection with the medulla oblongata, it being presupposed that in animals poisoned by prussic acid the central organs of the nervous system have lost the power of transmitting sentient impressions to motor nerves. But the result is perfectly satisfactory as far as regards the absence of motor power in the glosso-pharyngeus; for, since in all these experiments Dr. Reid found that muscular movements were excited by pinching the pharyngeal branch of the vagus, or the glosso-pharyngeal after it had received the communicating twig from the former nerve, the same stimulus applied to the glosso-pharyngeal before that branch of the vagus had joined it would have given rise to the same results if it had been endowed with motor power. The result obtained by Mr. Mayo might depend on his not having completely insulated the nerve from the pharyngeal branch of the vagus. Dr. Alcock, of Dublin, had found that after division of the glosso-pharyngeal nerves, the movements of deglutition were greatly impeded; but in Dr. Reid's experiments this effect was never induced, unless the pharyngeal branch of the par vagum was also divided; hence the pharyngeal branches of the glosso-pharyngeal nerve,

he remarks, cannot be the sole nerve by which the impressions, or peculiar sensations that induced the motions of deglutition, are communicated to the central organs of the nervous system.]

Nervus vagus cum accessorio Willisii.—At the point where the vagus passes through the foramen lacerum, its whole trunk swells into a ganglion; it thus presents every resemblance to the sensitive root of a spinal nerve; and, as immediately after its exit from the foramen it is joined by a portion of the nervus accessorius, it is in the present state of our knowledge very natural to suppose that the vagus, in fact, derives the motor fibres, which are distributed in its branches to the larynx and pharynx, from the nervus accessorius. Goerres,* indeed, had likened the origins of the vagus and spinal accessory to the two roots of spinal nerves, even before the discovery of the properties of their anterior and posterior roots. The same idea has been more recently adopted by Professors Arnold and Scarpa, who have compared the vagus to a posterior, the spinal accessory to an anterior root; and Bischoff† has carried it out, and adduced new arguments in support of this view.

The facts which are in favour of such an opinion are the following:

The spinal accessory divides below the ganglion of the vagus into an external branch which goes to the sterno-cleido-mastoid and trapezius muscles, and an internal which unites with the vagus.‡ From the trunk which is formed arises the pharyngeal branch of the vagus, but a portion of the accessory nerve continues its course in the substance of the vagus, and is supposed by Bischoff to afford the motor fibres of the laryngeal nerves, particularly of the nervus laryngeus inferior. M. Bendz has traced fibres of the spinal accessory into both the laryngeal nerves. The nervus accessorius exists in birds and reptiles. In the former it had been described by Serres, in the latter by Bojanus. Bischoff has examined it more accurately than any anatomists who preceded him, in several birds and reptiles. In birds it arises not

* Exposition der Physiologie. Coblenz, 1805, p. 328.

† Nervi Accessorii Willisii Anatomia et Physiologia. Heidelberg, 1832.

‡ [The vagus forms a second ganglion where it is joined by the internal branch of the spinal accessory. This second ganglion of the vagus, which has been described and figured by various anatomists since the time of Vieussens and Willis, but which was lately described by Mr. Cock (in the Guy's Hospital Reports for 1837) as a structure newly discovered by Sir A. Cooper, is, according to Bischoff, formed in mammalia by the vagus alone, the fibres of the nervus accessorius passing over it without entering into its formation; Beudz, however, has traced in the human subject a few fibres of the spinal accessory into this ganglion, and has found, on the other hand, that all the filaments of the vagus do not enter it. Branches of the sympathetic join the vagus nerve at the point where it forms its second ganglion, and if the superior ganglion of the vagus be regarded as analogous to the ganglion on the posterior roots of the spinal nerves, this inferior ganglion may perhaps belong to those enlargements formed by the sympathetic, where it unites with cerebral nerves. (See page 611.)]

between the anterior and posterior roots of the spinal nerves, but from the posterior columns of the spinal cord above the posterior roots, and its origin reaches inferiorly as far as the third cervical nerve. Superiorly, the nerve unites with the vagus, and forms with it the ganglion known as the ganglion of the vagus; so that here the accessory nerve merely contributes to form the vagus, which subsequently gives off a branch to the muscles of the neck, corresponding to the external division of the accessory in man: in the reptiles, also, the nervus accessorius is wholly united with the vagus. To these anatomical facts adduced by Bischoff, it may be added, that the vagus is evidently, in greater part, a nerve of sensation, and that the branches given to the stomach must be so entirely, since it is not possible by irritation of the vagus in the necks of animals to excite contractions of the stomach. (See pages 656 and 657.)

One only of the direct experiments of Bischoff is calculated to yield results from which satisfactory conclusions can be formed. He removed a portion of the occipital bone in a goat, and divided all the roots of the spinal accessory nerve on both sides. Even while he was cutting the radicle fibres of the nerve on one side, he remarked that the constant cry of the animal took a hoarser tone, which increased and became more and more marked as he divided the roots of the nerve on the left side. When all the origins of the nerve were divided, the voice was completely lost: "hircus omnem vocem amisit, et summissum quendam ac raucissimum tantummodo emisit sonum, qui neutiquam vox appellari potuit." This last observation is, however, not an absolute proof of the truth of the hypothesis. Such experiments will require repetition, unfortunately, before this interesting question can be decided. The method of testing the property of a nerve, which I have adopted in the case of the spinal nerves, namely, the application of mechanical and galvanic stimuli to their roots, must likewise be employed in this question, with reference to the accessory and vagus, to ascertain whether the irritation of the roots of either or both these nerves within the cranium will excite muscular contractions in the pharynx. I have, myself, performed one such experiment.

As the most speedy method, the cranium was laid open with a saw, and the arch of the first vertebra removed with bone forceps in a large living dog, in which the pharynx had been previously laid bare; the cerebellum was then cut away till the roots of the vagus and accessory nerves were exposed. They were now separated from their connection with the medulla oblongata, and the roots of the vagus irritated, as well mechanically as by means of the galvanic influence of a pair of metallic plates; a very distinct muscular contraction in the pharynx ensued. This result is unfavourable to the above theory; but I now place less confidence in it, for its value is not great

unless it were certain that none of the fibres of the glosso-pharyngeus were included with those of the vagus when the latter are irritated. But by a repetition of such experiments, in the way which I have described, the correctness or incorrectness of the theory might soon be decided.

[Dr. Reid has performed some experiments similar to the one just detailed, and with similar results: on applying the wires of the galvanic apparatus to the par vagum within the cranium, a distinct though feeble movement of the arytenoid cartilages followed, unattended by any movements of the shoulder; while irritation of the spinal accessory by galvanism within the skull, had given rise to powerful convulsive movements of the shoulder, but not the slightest movements of the previously exposed muscles of the glottis. In another dog a distinct movement of the pharynx and arytenoid cartilages followed the pinching of the insulated par vagum with the forceps. In a third dog convulsive movements of the pharynx accompanied the twitches of the shoulder when the spinal accessory was irritated.]

Although the valuable observations of Bischoff are strong arguments in favour of his opinion, yet there are some anatomical facts opposed to it which we must not conceal. The first is, the circumstance of the nervus accessorius arising more from the posterior than from the anterior part of the spinal cord, particularly in birds and reptiles. But this would not be an insurmountable objection, since it is not proved that the anterior and posterior columns of the spinal cord correspond in properties with the anterior and posterior roots of the nerves; and, moreover, the accessory nerve is evidently distributed to muscles. Another more weighty objection to the theory is founded on the relation which is often observed to exist between the accessory and the posterior roots of the cervical nerves. Mayer once saw a small ganglion on a fibre of the posterior root of the second and third cervical nerves, which was connected by a filament with the nervus accessorius. In some instances the same anatomist observed that the posterior root of the first cervical nerve was connected with the spinal accessory. * A case which I observed † was particularly interesting; the posterior root of the first cervical nerve was derived wholly from the accessory, and at the point where it was given off, a small ganglion was seated on the latter nerve. Hyrtl, also, has frequently observed a small ganglion on the spinal accessory nerve, when the posterior root of the first cervical nerve was not given off from it; it was then always situated opposite the entrance of the vertebral artery into the cranial cavity; Remak, likewise, has in one instance observed a small ganglion on the spinal accessory nerve in its passage through the foramen lacerum, and has shown it to me. Remak has moreover seen in the rabbit a portion of the fibres of

* Nov. Act. Nat. Cur. vol. xvi. p. 2.

† Müller's Archiv. 1834, p. 12; and 1837, p. 279.

the vagus pass over the ganglion which the rest of the nerve formed, without joining it.

I do not assert that the accessory nerve always contains sensitive fibres; I leave that question undetermined. But whenever the accessory nerve is closely connected with the posterior root of the first, or any other spinal nerve, we must suppose that it receives some sensitive fibres, as in the case in which I was able to demonstrate it; and every fact of that kind must render more probable the opinion of Monro,* that the connection of the accessory nerve with the posterior roots of the first and second cervical is an equivalent to it for a posterior root. The view which we ourselves take of the accessory and vagus nerves is this: the vagus corresponds, for the most part, to the posterior root of a spinal nerve; but we cannot, with certainty, affirm that it is wholly sensitive, since the experiment which we have detailed seems to show that its root contains motor fibres, and in some animals fasciculi of fibres of considerable size are seen to pass over the ganglion without joining it. Its composition may possibly be just the reverse of the ninth, or lingual, which is in greater part, but not wholly, a motor nerve. The accessory is probably chiefly motor, and is more analogous in structure to the anterior roots of a spinal nerve; but evidently contains, in many cases, (perhaps in all,) sensitive fibres, derived either from its own roots, or from the posterior roots of the first and second cervical.† [Dr. Reid found that when the external branch of the spinal accessory was strongly compressed between the blades of the forceps, or firmly included in a ligature, the animal gave very decided evidence of suffering pain; but he does not pretend to determine whether the sensitive filaments on which this result depends belong originally to the nerve, or whether it derives them from other nerves at the base of the cranium. The experiments of Professor Müller, and those of Dr. Reid, detailed above, prove that the trunk of the vagus contains within it motor filaments, independent of those which it receives from the internal branch of the spinal accessory; while Dr. Reid's experiments also show that this internal branch of the accessory certainly assists in moving the muscles of the pharynx.]

The vagus affords sensitive influence to all the parts to which it is distributed; namely, the organs of voice and respiration, the pharynx, œsophagus, and stomach: moreover, it gives a sensitive branch, which penetrates the petrous portion of the temporal bone, to the external ear,—the ramus auricularis; and the facial nerve probably derives its sensitive endowment from its connection with this branch of the vagus within the temporal bone.

* On the Nervous System, 1783.

† Compare Bendz, De connexu inter vagum et accessorium, Havn. 4. An abstract is given in Müller's Archiv. 1837. Jahresb. p. xxviii.

The branches of the vagus, which are motor as well as sensitive, are the pharyngeal and laryngeal. Division of the inferior laryngeal nerve, or of the vagus in the neck on both sides, paralyses incompletely the small muscles of the larynx; the voice is lost, but is regained in a few days, from the superior laryngeal nerve continuing to exert its influence. The assertion of Magendie, that the superior laryngeal nerve is distributed solely to the contractors of the glottis, and the inferior to the dilators, was not confirmed by Schlemm's dissections. The vagus has no motor influence on the stomach; neither by galvanism, nor by mechanical irritation applied to the nerve in the neck, can motions of the stomach be excited: this results from the experiments of Magendie, Mayo, and myself.

[With respect to the motor and sensitive properties of the individual branches of the vagus, we learn from the experiments of Dr. Reid: 1. That the pharyngeal branch in the dog is the principal, if not the sole motor nerve of the constrictors of the pharynx, the stylo-pharyngeus muscle, and the muscles of the soft palate, and that it is most probably wholly motor: in six out of seven experiments, no decided evidence of suffering was given when this nerve was irritated, pricked, cut, or tied; in the seventh case there was, perhaps, some unusual distribution of nervous filaments. 2. That the inferior laryngeal nerve is the motor nerve of the larynx, irritation of it producing vigorous movements of the arytenoid cartilages; while irritation of the superior laryngeal nerve (by galvanism) gave rise to no action in any of the muscles attached to the arytenoid cartilages, but merely to contractions of the crico-thyroid muscle; this result agrees with their anatomy. Dr. Reid found that the internal branch of the superior laryngeal nerve was distributed almost entirely to the mucous surface of the epiglottis and interior of the larynx, and its external branch to the crico-thyroid muscle, a few filaments being also sent to the inferior constrictor of the pharynx and to the thyro-hyoid muscle; while, on the contrary, the recurrent nerve sends but few filaments to the mucous surface of the larynx; one or two from the branch which, after sending ramifications to the mucous surface of the pharynx, anastomoses with the external branch of the superior laryngeal, can be traced to the crico-thyroid muscle, and the rest, with the exception of some which reach the mucous membrane of the trachea, are distributed to the muscular fibres of the trachea, to the crico-arytenoideus posticus, crico-arytenoideus lateralis, thyro-arytenoideus, and arytenoid muscles. Experiments on living dogs showed also that division of the recurrent nerves puts an end to the motions of the glottis, but that the sensibility of the mucous membrane remains; that division of the superior laryngeal nerves leaves the movements of the glottis unaffected, but deprives it of its sensibility. The superior laryngeal nerve, therefore, is chiefly sensitive; the inferior, for

the most part, motor. 3. Œsophageal branches.—Dr. Reid found, as had been done by previous observers, that irritation of the trunk of the vagus excited motions of the œsophagus, which extended over the cardiac portion of the stomach; and that division of the vagus paralysed the movements of the œsophagus, which became distended with the food which was afterwards taken. The motions of the œsophagus, then, are dependent on motor fibres of the vagus, and are excited by impressions made upon sensitive fibres, probably of the vagus also, as Dr. Reid supposes. Dr. Reid confirms the statement, which had been denied by Dr. Marshall Hall and Mr. Broughton, that pinching the vagus nerve in the neck gives rise to pain. 4. The cardiac branches of the nerve are believed by Dr. Reid to be one channel through which the influence of the central organs is transmitted to the heart; for he found the effect of crushing the brain with a hammer, in rabbits, to be much less marked when the vagi nerves had been previously divided. 5. Again, from the continuance of the respiratory movements after the division of the vagi nerves,* he infers that the pulmonary branches of the vagus form only one channel, by which the impressions on the mucous surface of the lungs that excite respiration are transmitted to the medulla oblongata; the other channel being furnished by the sympathetic, which conveys the impression to the spinal cord. The effusion into the lungs, which ensues after the division of the vagi, Dr. Reid believes to be the consequence, not the cause, of the dyspnœa; and this dyspnœa he is inclined to attribute to the paralysis of the muscular fibres of the bronchi.]

Nervus hypoglossus, lingualis, or ninth nerve. — In the ox, and some other mammalia, in which Mayer has discovered that this nerve has a small posterior root with a ganglion, it belongs to the mixed nerves with double origin; but in the human subject it has merely a motor root.

That it is principally a motor nerve, the experiments of Magendie, Mayo, and myself demonstrate. † Violent spasms of the whole tongue, even to the tip, are excited by stretching, pinching, or by galvanising it with a single pair of plates. Its division in a living animal deprives the tongue of its power of motion. This nerve, therefore, supplies the motor influence for the motions of the tongue in deglutition and in articulation. A case related by Montault at the Academy of Medicine at Paris is illustrative. The symptoms were spasm and tremor of the muscles of the neck; pain on the left side of the head and neck, and difficulty of articulation with gradual wasting of the tongue, which, when protruded from the mouth, was drawn towards the right side. The left side of the tongue was most wasted, but taste was perfect on both

* [See Dr. Hall's explanation in the chapter on the reflected motions, page 715.]
† See Froriep's Notiz. No. 647.

sides. At a later period there were difficult deglutition, aphonia, and other symptoms. After death an hydatid cyst was found in the left occipital fossa, which raised the left lobe of the cerebellum and pushed the medulla oblongata to the right side, extended a few lines into the spinal canal, and was imbedded in the anterior condyloid foramen, while a prolongation from its base passed through the anterior part of the foramen lacerum posterius. From the point of their exit from the cranium, the left hypoglossal and glosso-pharyngeal nerves were atrophied; the vagus and spinal accessory were not affected.

The lingual is also the motor nerve of the large muscles which move the larynx.

Desmoulins, Magendie, and Mayo assert, that the hypoglossal nerve is likewise endued with sensibility; pain is produced, they say, by stretching it in dogs and cats. In dogs, this might be accounted for by its small posterior root; but in the cat Mayer has found no posterior root; and, in this instance, its sensitive faculty may be due to sensitive fibres received from other nerves in its course, for instance, in its connections with the nervus vagus, and with the first cervical nerve.

Nerves, for the most part motor, and without a ganglion on their root, but which contain within themselves sensitive fibres, or receive them in their course from other nerves.

Nerves of the muscles of the orbit. The third, fourth, and sixth.—These nerves have some sensitive endowment. The sensibility which muscles generally possess, can in other instances be ascribed to the sensitive fibres derived from the posterior roots of the nerves, and distributed with the motor fibres to the muscles. But this explanation is inapplicable in the case of the muscles of the eye. It is known to every one, that violent action of these muscles is attended with the sensation of an unpleasant tension in them. Is this owing to the single motor non-gangliated roots of the nerves of these muscles containing sensitive fibres, or do the nerves receive sensitive fibres from other sources in their course? The nervus trochlearis has been frequently seen to be connected with the first division of the fifth; I have myself seen, in the calf, a twig given off to the trochlearis from the latter nerve. It is not known whether the sensitive fibres of the longer root, which the ciliary ganglion derives from the nasal branch of the fifth, are all distributed in the ciliary nerves; or whether some reach the short root of the ganglion, and thus the motor oculi nerve. The sixth, or abducens nerve, can apparently derive no sensitive fibres from other nerves. Under these circumstances it must remain undecided whence these nerves acquire the fibres by which they are endued with sensitive power.

Nervus facialis, or portio dura of the seventh nerve.—This is the special

motor nerve of all the muscles of the face, (the muscles of mastication excepted,) of the occipito-frontalis, the muscles of the ear, the stylo-hyoid muscle, the posterior belly of the digastricus, and the platysma myoides. Division of the facial nerve in mammalia paralyses each and every one of the muscles of the face: the eyebrows cannot be raised, nor the eyes closed; the muscles of the ear do not act, and the nostrils are motionless, &c. Experiments which establish this have been instituted by Bell, Mayo, Schoeps, Backer, myself, and others. Backer remarked, in an animal poisoned with nux vomica, that division of the facial nerve put a stop immediately to the spasms in the muscles of the face, although they continued in other parts of the body.

I have myself instituted experiments with a view to determine the properties of this nerve.* I irritated it with a needle, and pinched it with a pair of forceps, and most distinct twitchings of the muscles ensued, occupying the nostrils or eyelids, according to the branch of the nerve which I thus treated. Galvanism by means of a single pair of plates had the same effect as mechanical stimulus. These facts prove that the facial is a motor nerve, and the pathological cases observed by Sir C. Bell confirm this result.

A man received a ball from a pistol in the ear, and the facial nerve was wounded at its origin. The motion of the same side of the face was lost, sensation preserved. The second case was that of a man who had been wounded by the horn of an ox at the point of exit of the facial nerve. The whole side of the face was deprived of motion, the eyelids remained open, the angle of the mouth distorted, the ala of the nose in deep inspiration motionless, and the muscles of that side of the face had, in fine, become atrophied. The sensibility of the paralysed parts was not defective. Again, the facial nerve was divided in extirpating a swelling situated in front of the ear. The result was the same as in the other cases.

Sir C. Bell imagined that certain muscles of the face, for example, those of the lips and nostrils, might lose their power of motion in the expression of the passions, but might still perform their part in the movements of mastication, and *vice versâ;* and he explained this by the circumstance of these muscles receiving branches both from the facial and the infra-orbital nerve. But the latter nerve has not the slightest motor power, and the muscles of the face are, by division of the facial nerve, rendered incapable of any kind of motion; the special muscles of mastication are not paralysed, because they are supplied by the motor portion of the fifth nerve, not by the facial.

[In two cases of injury to the portio dura within the temporal bone, Mr. Shaw has observed partial paralysis of the soft palate. With the usual distortion of the face, &c., there was the peculiarity of the uvula being drawn towards the paralysed side during inspiration.†]

* See Froriep's Notiz. No. 648.

† Med. Gaz. Sept. 1837.

Sir C. Bell regarded the facial nerve as motor only, but it is also highly sensitive.

Division of the facial nerve was observed by M. Schoeps to be productive of no pain in the rabbit, but of considerable suffering in the cat. Here, however, this observer must have been mistaken; for, in my experiments on rabbits, I have found the animals suffer so much pain as to utter loud cries when the facial nerve was divided. Magendie also observed that the division of the nerve produced more or less pain. A slight sensibility was observed by Mr. Mayo in the facial nerve of the ass; in the horse, dog, and cat, it was very marked. Backer also found the division of the nerve in cats to be always productive of pain.* Eschricht has made the same remark.

The sensibility of the nerve is indubitable; but whether its sensitive fibres are contained in the nerve itself from its origin, or superadded to it in its numerous anastomoses with the fifth nerve, namely, with the superficial temporal, subcutaneus malæ, infra-orbital, and mental branches, is another question. Eschricht has adopted the latter view. He divided the nervus trigeminus within the cranium; the facial nerve was still sensible to pain. In a second experiment, he divided the nervus trigeminus on the left side; the facial nerve was no longer sensible on that side, while on the other it retained its sensibility. In a third experiment, Eschricht divided the left nervus trigeminus, and observed that the anterior part of the facial nerve of the same side was by this deprived of sensibility, which however was still retained by the posterior portion of the facial nerve where it is situated under the meatus auditorius externus. From this, and a similar experiment, Eschricht inferred that the nervus trigeminus supplies sensibility to the anterior part of the facial, not to its posterior part. That the union of the several branches of the facial nerve with branches of the infra-orbital is not the source of the sensibility of the facial nerve behind the points of anastomosis, is proved by a very good and simple experiment of M. Gaedechens in the dog. After dividing the branches of the facial nerve which unite with the infra-orbital nerve, he found the latter [query, former] nerve still sensible to pain. In another experiment, he divided a considerable branch of the facial, which united with the infra-orbital nerve, and then found the portion of the divided branch which he had separated from the trunk of the facial insensible; this branch, therefore, must have derived its sensibility, not from the infra-orbital nerve with which it was still connected, but from the facial nerve itself, or from branches of the nervus trigeminus situated much more posteriorly,—such as the superficial temporal branch, which is connected with the facial nerve, in front and below the external ear.

Eschricht's experiments have at all events proved that the facial nerve

* Loc. cit. p. 64.

does not derive all its sensitive fibres from the nervus trigeminus. Some have, therefore, supposed that it has itself two roots, consisting of different kinds of fibres, and belongs to the mixed nerves. The portio intermedia Wrisbergi, in the origin of the facial nerve, has been regarded as a separate root; and the swelling on the nerve, where it makes its angular bend, as a ganglion of a sensitive nerve.* This enlargement of the nerve is situated, however, at the point where it is joined by filaments which connect it with the sympathetic, and is analogous to the spheno-palatine ganglion on the second branch of the nervus trigeminus. The nervous filaments which join the facial at the point indicated, are the nervi petrosi superficiales major et minor, and the nervus petrosus superficialis, discovered by Bidder.† The mere existence of the portio intermedia Wrisbergi does not prove that the nerve has a second sensitive root; the second root should have a ganglion upon it; for, if every separate fasciculus in the origin of a nerve were regarded as a root with distinct properties, the spinal accessory would have several, indeed many functions; the hypoglossal nerve, in many cases, two; and the olfactory nerve, three.

We must, therefore, admit that the facial nerve is at its origin simply motor, or that it receives sensitive fibres from the brain without having a special sensitive root. The last supposition is not necessary, however; for the source can be distinctly shown from which the facial nerve derives the sensibility which it still retains at its exit from the stylo-mastoid foramen when the trunk of the nervus trigeminus is divided. A branch of the vagus, namely, unites with the facial nerve in its course through the Fallopian aqueduct; this communicating branch of the vagus, which exists in man as well as in animals, and which completely explains all difficulties, was first discovered in the human subject by Comparetti,‡ and has been also described by Cuvier§ in the calf. A considerable branch is given off from the nervus vagus at an acute angle, and passes through a special bony canal to the facial nerve, with which a portion of its filaments unites; while the continuation of the branch is distributed to the external ear. This nerve, which we have seen in the calf as well as in the human subject, is evidently a principal cause of the sensibility of the facial nerve.

CHAPTER III.

OF THE SENSITIVE AND MOTOR PROPERTIES OF THE GANGLIONIC NERVES.

1. *The ganglionic nerves are sensitive.*—Some observers have denied to the sympathetic the property of conveying sensations. Bichat states,

* Gaedechens, Nervi facialis Physiol. et Patholog. Heidelb. 1832.

† See Müller's Archiv. 1837. Jahresb. p. xxvi.

‡ De Aure internâ. Patavii, 1789, p. 109. 133.

§ Anat. Comparée.

that he irritated the cœliac ganglion both mechanically and by chemical stimuli without exciting pain. Dupuy cut out the inferior cervical ganglion, and the animals, he says, did not suffer. Wutzer* also could excite no pain by irritating the lumbar ganglia in a dog. The observations of Magendie and Lobstein agree with the foregoing. Flourens,† on the contrary, has in such experiments always observed more or less distinct signs of pain. In Brachet's‡ experiments there were sometimes manifestations of suffering, sometimes none. Mayer § has observed, that both when the superior cervical ganglion was divided, and when the solar plexus was irritated, the animals gave distinct evidences of pain. With these last observers, my experiments lead me to agree entirely. I have not only several times seen distinct signs of suffering produced by the application of mechanical and chemical irritants to the cœliac ganglion, but, in all the experiments of tying the nerves of the kidneys which I performed in conjunction with Dr. Peiper (see page 471), I observed evident signs of considerable pain. The painful sensations felt in diseased states of the parts supplied with sympathetic nerves only, prove, much more clearly than experiments can do, that these nerves have sensitive endowments. I must give my complete assent to the following remark of Prof. E. H. Weber: "I, for my part, regard the daily observations of the existence of pain in these parts, which some would deny to be sensible, as far more worthy of attention than the foregoing experiments."||

The sensibility of the parts supplied by the sympathetic is, however, far more feeble and indistinct than in other parts; for we seldom feel in the stomach the very cold or hot food which we swallow: substances, too, which are strong stimulants of the skin, such as mustard and horse-radish, are rarely productive of sensation in the parts furnished with sympathetic nerves; it requires very strong impressions to excite the whole sensitive power of these parts in as powerful a degree as can be done in other organs. This peculiarity has been explained on the hypothesis of Reil, that the ganglia have the nature of half-conductors, preventing the transmission of weak impressions, and allowing the transmission of such only as are the effects of very intense irritation. Although this view cannot be strictly demonstrated to be correct, yet it is apparently favoured by an observation of Brachet,¶ relative to the effects of irritation of the thoracic ganglia of the sympathetic in a living sheep. Brachet states that, having divided the costal cartilages on the right side near the sternum, he held the lung towards the sternum, and then saw the thoracic ganglia of the sympathetic at the sides of the spinal column. When he pricked the ganglia, or the cord

* De Gangl. fabricâ. Berol. 1817.

† Expér. sur le Système Nerveux.

‡ Recherches sur les fonct. du syst. nerv. gangl. p. 307.

§ Act. Nat. Cur. xvi. p. 2.

|| Hildebrandt's Anat. t. iii. p. 355.

¶ Loc. cit. p. 307.

of the sympathetic between them, he perceived no signs of pain; but, when he irritated one of the branches of communication between the sympathetic and the spinal nerves, pain was distinctly manifested: this he witnessed in repeated experiments. He also observed, that ganglia, which at first appeared to be devoid of sensibility, became sensible after frequent irritation.

2. *The ganglionic nerves have a motor, though involuntary, influence on the parts which they supply.*—The experiments which I performed with Dr. Sticker have proved that the contractile power of the muscles is the result of a reciprocal action between them and the nerves, and that in a short period after division of the latter it is, like the excitability of the nerves themselves, lost, provided reunion has not taken place; it is evident, therefore, that the contractions of the voluntary muscles must be under the influence of their nerves, and not a property of themselves as muscles, as Haller supposed. We have, likewise, some direct proofs of the motor influence of the ganglionic nerves on the muscles. Humboldt has excited contractions of the heart in mammalia, by the application of galvanism to the cardiac nerves. Since his experiments were performed with the simple galvanic circle, they are certainly of great weight. Burdach* likewise states, that the pulsations of the heart in a dead rabbit, in which artificial respiration was kept up, became stronger when he applied galvanism to the cervical portion of the sympathetic nerve, or to the inferior cervical ganglion. In another rabbit, he says, the action of the heart was accelerated by the application of caustic potash or ammonia to the nerve; this experiment I have repeated without a successful result. Wutzer† applied the poles of a galvanic pile to the second lumbar ganglion insulated by a piece of glass placed beneath it, and states that all parts of the abdomen, and even the muscles of the thigh on the corresponding side, were thrown into tremors in consequence; and I have myself seen the peristaltic motions of the whole intestines in a rabbit accelerated, and renewed when they had already ceased, by the application of the poles of a galvanic battery of sixty-five pairs of plates to the peripheral portion of a splanchnic nerve previously divided and insulated on a plate of glass. These last experiments of Wutzer and myself do not however really prove much, and are faulty, inasmuch as the galvanic stimulus employed was too powerful; the galvanic fluid might have been transmitted through the nerve, as a mere moist conductor, to the intestine itself; and the experiment was really the same as if the poles had been applied directly to the intestines. In fact, in Wutzer's experiment the galvanic fluid (not the nervous principle) reached the nerves of the lower extremity, or the lumbar and sacral plexus. A more satisfactory proof of the motor power of the

* Physiol. Bd. iv. p. 464. † Loc. cit. p. 127.

sympathetic is the experiment which I have frequently instituted, and constantly with the same result, on the cœliac ganglion in the rabbit. The abdomen of a rabbit being opened, I waited until the active motions of the intestines excited by the influence of the atmosphere had subsided again, or ceased, and then touched the cœliac ganglion with caustic potash, when the peristaltic motions were immediately renewed with extraordinary activity.

Composition of the sympathetic nerves.—The question now presents itself, whether there are in the ganglionic nerves fibres of one kind only, and whether these perform all the functions of nutrition, sensation, and motion; exciting sensations by their action on the brain, and nutrition and motion by an influence transmitted in the peripheral direction. This is in itself improbable; for, were it the case, the excitement of secretion in the intestinal canal would always be attended with increased motion, and increased motion with increased secretion. This consideration is alone sufficient to suggest the probability that even in the ganglionic nerves there are sensitive and motor fibres; and, moreover, a third kind of filaments, organic fibres, namely, for the regulation of the chemical processes. To determine this question with greater certainty, we must more accurately consider the connection which exists between the sympathetic and the sensitive and motor nerves.

It has been long disputed whether the communicating cords between the ganglionic nerves and the trunks of the cerebral and spinal nerves are to be regarded as the roots of the sympathetic, or as branches of communication given off from it. The microscopic analysis of these intermediate cords has shown that many of them convey to the sympathetic nerve radicle fibres from the cerebro-spinal nerves; that others, on the contrary, consist of fibres passing to the latter nerves from the sympathetic. Thus, it will subsequently be shown, that the carotid portion of the sympathetic is not merely a root of that nerve; that it is, on the contrary, chiefly composed of elements of the sympathetic going to be superadded to the cerebral nerves, to be distributed with them in the peripheral direction. The portions of the carotid plexus which join the first and second branches of the fifth nerve and the nervus abducens, convey to these nerves fasciculi of grey fibres which are distributed in their ramifications; and these grey fasciculi are not roots of the sympathetic. On the other hand, the sympathetic receives true roots from other cerebral nerves, (particularly those with double origin,) and from all the spinal nerves; these roots are derived from the radicle fibres of the nerves from which they come off, and enter the sympathetic to be distributed in the peripheral direction in it.

The relation of the sympathetic with the cerebral nerves is very

complicated, its connection with the spinal nerves is simple and easily made out. The investigation of its communications with the latter affords us principles by which the nature of its connections with the cerebral nerves may be determined. It can be seen without difficulty, in any animal, that from the roots of every spinal nerve a portion is given off to join the ganglionic nerves. This forms the ramus communicans. Its fibres run, for the most part, *from* the spinal nerves *to* the ganglionic nerve.

But do these roots supply the ganglionic or sympathetic nerve with both motor and sensitive fibres from the spinal cord and brain? Scarpa and Wutzer inferred, from their earlier researches, that the sympathetic is connected with both roots of each spinal nerve, and consequently receives both sensitive and motor fibres, which the functions of the viscera dependent on its influence show that it must contain. The sensibility of such parts is certainly not very great, and the sensations cannot be referred to a distinct and circumscribed spot; but in diseases they become as strong and defined as in any other parts. The movements of the parts supplied with ganglionic nerves is also involuntary only; and this circumstance led Scarpa more recently into the error of denying all motor influence to the sympathetic, and to place the cause of the involuntary movements of such parts in the organs themselves. He grounded this view especially on his later dissections, in which the sympathetic appeared to him to derive filaments from the posterior roots only of the spinal nerves.* This great anatomist did not, even in his old age, (as some do, even before that time,) become prejudiced against the advances which science made; in his last work he evinced the greatest interest in the revolution which the physiology of the nervous system was undergoing: but, in his assertion relative to the origin of the sympathetic, he was in error; for the investigations of myself,† of Retzius,‡ Mayer,§ and Wutzer,|| have established as correct the view which Wutzer had formerly taken, namely, that the sympathetic derives radicle fibres from both roots of the spinal nerves. Mayer has indeed traced these fibres in the roots of the nerves as far as the spinal cord itself. The sympathetic contains, therefore, both motor and sensitive fibres.

By the microscopic examination of the radicle fasciculi derived by the ganglionic nerve from the spinal nerves, it is learnt that they consist of cylindrical fibres, similar to those which compose the spinal nerves themselves: the tube and its contents are as easily distinguished. These fibres are, however, more minute in their whole course in the gang-

* Scarpa, De gangliis nervorum, deque essentiâ nervi sympathici.—Ann. Univ. de Medicinâ, 1831.

† Meckel's Archiv. 1832, p. 85.

‡ Ibid. p. 260.

§ Nova Acta, xvi. p. 2.

|| Müller's Archiv. 1834, p. 305.

lionic nerves than they are in the spinal nerves; and they are of more delicate texture, and hence more prone, under pressure or extension, to form varicosities; but, when they have suffered no mechanical violence, they are never varicose. In these respects, therefore, as well as in the circumstance that the cylindrical fibres in it do not anastomose, but remain separate in their course, the sympathetic does not essentially differ from other nerves. The peculiarity of the sympathetic seems to consist merely in the mode in which it assembles its radicle fibres, and again distributes them in the peripheral direction. The radicle fibres run, namely, for a certain extent in the principal cord of the sympathetic before being given off in the branches; and thus is produced an apparently continuous cord from the superior cervical ganglion to the ganglion coccygeum. I say, apparently continuous; for there are no facts to justify the conclusion that the fibres coming from the first cervical ganglion are continued to the inferior extremity of the cord. The fibres leave the longitudinal cord in the same order as they enter it: the first form the cardiac nerves, the next the splanchnic, the next the renal, the aortic, and so on. This relation of the fibres to the principal cord of the sympathetic may be compared to the mode of attachment of the sacro-lumbalis muscle to the ribs. But it is not really a peculiarity of the sympathetic. It is a structure common to many other nerves; the spinal nerves, for example, have arches of communication between each other, and thus form continuous cords, extending a considerable distance, from which are given off in succession the nerves which had previously joined them. The nerve called the ramus descendens noni, again, is partly formed by the superior spinal nerves. On the other hand, it sometimes happens that the cord of the sympathetic is interrupted here and there between the points where the radicle fibres join it, or is extremely thin, as in serpents.

It being shown that the sympathetic regularly receives fasciculi of motor and sensitive fibres from the spinal nerves as its motor and sensitive roots, the existence of a similar relation between it and those cerebral nerves which are analogous to the spinal nerves, in having double roots, becomes very probable. The hypoglossal, vagus, and glossopharyngeal nerves do in fact give roots to the superior cervical ganglion, and thus to the cord of the sympathetic. We do not, however, mean to assert that all the fibres of these cords are motor and sensitive, for such is not the case. The ganglionic or sympathetic nerve, then, receives roots of sensitive and motor properties from the cerebral nerves which we have named. It likewise receives a similar root from the great spinal nerve of the head, the nervus trigeminus. The vidian nerve is, at least in part, a root given off to the sympathetic, as will be more distinctly proved in the following chapter.

CHAPTER IV.

OF THE SYSTEM OF GREY OR ORGANIC FIBRES, AND ITS PROPERTIES.

In the present state of our knowledge, little instruction can be derived from the views of the earlier physiologists relative to the properties of the sympathetic or ganglionic nerves. It is not sufficient to be told that these nerves are destined for the supply of the vegetative system of the viscera, while the cerebro-spinal nerves supply the animal system ;—that they have the office of uniting the nerves, one with another, into one harmonious whole ;—or, that they are the cause of the sympathies. The important labours of Sir C. Bell, relative to the sensitive and motor roots of the nerves, left us in ignorance concerning the sympathetic; but they suggested to intelligent minds the necessity of a complete reform of our notions regarding this nerve. It is but recently that the facts and ideas contributing to this reform have been published. The earliest that I am acquainted with were made known by Retzius in 1827. He made the remark, that there were grey fibres mixed with the white in the nervus trigeminus; and that these grey fibres issued from certain ganglia, and ran both in the peripheral direction in the branches of the nerve, and also in the central direction, towards the Gasserian ganglion. Retzius himself deduced no physiological conclusions from these important facts. They remained without further application until the year 1834, when a more definite exposition of the principles according to which the ganglionic or sympathetic nerve, and its connections with other nerves, are to be regarded, was published by Van Deen and by myself. Van Deen* laboured to render probable his opinion, that the communications of the ganglionic with the cerebro-spinal nerves are destined to impart to the latter a vegetative influence, in addition to their sensitive and motor properties; and to the ganglionic nerve a motor influence, and also the faculty of sensibility to impressions under certain circumstances. Van Deen was not acquainted with the facts observed by Retzius; and he does not explain his views as to the nature of the connections between the ganglionic and cerebro-spinal nerves—whether the ganglionic nerve is merely brought into closer relation with the latter nerves by means of its ganglia, or whether it continues its course in them without uniting with their fibres.

I founded my opinions on the observations of Retzius and my own investigations relative to the presence of organic grey fibres running in the peripheral direction in the cerebral nerves—on the fact of the primitive fibres of nerves not uniting with each other in their course—on the origin of the ganglionic nerve from the motor and sensitive roots of the

* Diss. de differentiâ et nexu inter nervos vitæ animalis et organicæ. Lugd. Bat. 1834.

spinal nerves—and on the facts relative to the reflex actions of the nervous system I expressed* my conviction, not merely that the commonly-received notions respecting the supposed use of the connections of the ganglionic with other nerves—namely, the transmission of sympathetic influences,—are erroneous; but that the ganglionic, as well as the cerebro-spinal nerves, are compound in structure. I suggested that they contain motor, sensitive, and organic fibres, of which the latter kind alone have the function of regulating the vegetative processes, and have a special relation to the ganglia; that the cerebro-spinal nerves are likewise composed of motor, sensitive, and organic fibres, of which those of each kind have their specific destination, and run their course together without uniting with the others; that the ganglionic nerve consequently differs only in having numerous ganglia, and in containing a larger number of grey fibres, which give it a proportionally greyer colour; while, in the cerebro-spinal system, the grey fibres are less numerous, and are seen as grey fasciculi lying in the larger mass of white fasciculi. The ganglionic nerve is not, however, I observed, equally grey in all parts; the main lateral cords are whitish; the branches of the abdominal ganglia, which are distributed to the viscera of vegetative life, principally grey. This is the history of the progress of our knowledge of this subject up to the present time. Remak has brought it to a state of far greater certainty.

1. *Grey or organic fibres in the cerebro-spinal nerves.*—The facts relative to this subject, which were given in the first edition of this work, are the following:—First, the remarkable and important observation of Retzius,† that in the nervus trigeminus of the horse, and particularly in the second division of the nerve, there are distinct grey sympathetic fibres, derived from the spheno-palatine ganglion, which form small grey ganglia within the nerve, and can be traced over the second division of the nervus trigeminus, and within it, as far as the nasal nerves and pituitary membrane, as well as upwards into the orbit and to the ciliary ganglion. I have examined these gangliated nerves of Retzius in the ox; they are there easily found, and form on the inner side of the second division of the fifth nerve several small ganglia, which are connected with the spheno-palatine ganglion and the vidian nerve, and belong principally to the nerves going to the nose and palate. In the ox the deep branch of the vidian, derived distinctly from the sympathetic, gives some fibres to the spheno-palatine ganglion, and likewise many filaments, which accompany the nasal and palatine nerves; and here it may be distinctly seen, that a part of the fibres of this nerve is derived, not from the nervus trigeminus, but from the sympathetic, and that it gives branches which attach themselves to, and accompany in the peripheral direction,

* In the second part of the first volume of the Handbuch der Physiologie, published in 1834; p. 646—652, and p. 780.

† Isis, 1827, p. 997.

the branches of the second division of the fifth. In the ox it is also very easily seen, that the first division, likewise, of the fifth nerve receives organic fibres from that part of the sympathetic which joins the nervus abducens; and there are small ganglia on the commencement of this division of the fifth nerve, which belong to the organic fibres. Grey fibres pass backwards, also, to the Gasserian ganglion.

In the human subject, too, fibrils have been seen by Varrentrapp* to be given off from the cavernous plexus to the first division of the nervus trigeminus. Moreover, in the calf, there is, as I have seen, a thick fasciculus of organic fibres, sent from the sympathetic within the cranium to join the second division of the fifth nerve, just below the Gasserian ganglion. The buccinator branch of the third division of the same nerve receives in the ox, from the ganglion oticum, a whole fasciculus of grey organic fibres, which accompany the nerve in its peripheral distribution. In the ciliary nerves, arising from the ciliary ganglion, we have a further example of the association of sensitive fibres from the fifth nerve, motor fibres from the third, and organic fibres from the sympathetic. The connection of the sympathetic with the glosso-pharyngeal nerve, at the point where the ganglion petrosum is formed, and with the facial nerve at the situation of its enlargement in the Fallopian canal, seems to be for the purpose of superadding organic fibres to these nerves. From the point where the facial makes its bend, and is swollen, it is rendered larger than before by the fasciculi which it receives from the superficial petrosal branches of the vidian; and this increased size is in part still distinctly observable in its peripheral continuation.

Several new facts have been made known by M. Giltay,† showing that organic fibres can be traced accompanying cerebral and spinal nerves as far as the organs to which they are distributed. In several fishes he saw distinctly that the cephalic portion of the sympathetic, which arises from the nervus trigeminus without the cranium, and passes backwards beneath the glosso-pharyngeal and vagus nerves, gave off organic fibres which joined the nervus glosso-pharyngeus, accompanying it as far as the first branchia, while a separate fibre from the same source accompanied the vagus to the branchiæ; the sympathetic fibres were here quite separate from the branches of the cerebro-spinal nerves, and merely ran side by side with them. M. Giltay has seen and represented these facts distinctly in fishes of the genera acanthurus, platycephalus, and holocentrus, and less distinctly in the pleuronectes platessa. The branches of the sympathetic here referred to must not be confounded with the communicating fibres from the glosso-pharyngeal nerve and the ganglion of the nervus vagus, which are as it were roots of the sympathetic.

* Obs. anat. de parte cephalicâ n. sympathici. Francof. 1831.

† De nervo sympathico diss. Lugd. 1834.

M. Giltay has in a few cases observed a similar relation of organic fibres to spinal nerves. In the bufo asper he saw the sympathetic on the middle of the body of the second vertebra, under the point of attachment of the shoulder, give off to the muscles (?) a branch which divided into two twigs; one of which took a retrograde course on the first dorsal nerve towards the vertebra, and seemed therefore to be a root of the sympathetic, the other accompanied the nerve in its course to ramify in the anterior extremity. In the calotes gutturosa, M. Giltay saw a branch of the sympathetic accompany the subclavian artery and the nerves of the anterior extremity, to ramify in the latter. In the iguana delicatissima also, he found a twig from the sympathetic accompanying the first nerve of the anterior extremities.

From all the foregoing facts I arrived at the conclusion that in the cerebro-spinal nerves three kinds of fibres must be distinguished; the sensitive and motor, which are both white, and come from the roots of the cerebro-spinal nerves,—and grey organic fibres, which have their origin in the ganglia of the ganglionic or sympathetic nerve itself.

The observations of Remak have made us acquainted with the peculiar microscopic characters of the grey fibres, by which they may be distinguished from the tubular sensitive and motor fibres. They are, namely, much more minute; a high magnifying power is required in their examination; are perfectly homogeneous, that is to say, not composed, as far as can be distinguished with the microscope, of a tube and contained portion; they are so pale and transparent, that unless a strong shadow be thrown on them they are not visible; lastly, a completely characteristic appearance is produced by the small roundish or oval bodies which here and there beset their surface. Remak has detected these fibres in the grey fasciculi in many parts of the sympathetic, and has seen perfectly similar fibres more rarely inmany cerebro-spinal nerves. To convince one's self of the existence of this peculiar system of fibres, they must be first examined in a completely grey nerve, in which they are mingled with but very few, if with any, cylindrical fibres. I took the perfectly grey nervous cord which leaves the carotid plexus at the inner side of the Gasserian ganglion, in the calf, to join the first division of the fifth nerve and the nervus abducens. I found it composed nearly entirely of organic fibres such as those just described. Here and there a single tubular fibre was seen running over an entire fasciculus of grey fibres, and by the contrast making the difference between them more evident.

All the grey nervous fasciculi which we have described as accompanying in their peripheral distribution the first and second division of the fifth nerve, are composed of such fibres. The grey fibres are also contained in the grey fasciculi, which, coming from the otic ganglion, or plexus gangliiformis Santorini, accompany the third division of the fifth nerve, and particularly the buccinator branch. In other parts of the

cerebro-spinal system such favourable opportunities are not afforded for becoming acquainted with the characters of the organic fibres, and it requires a practised eye to recognise them when they are mingled scantily with the more numerous cylindrical fibres. Remak found a few grey fasciculi in most of the cerebro-spinal nerves which he examined. The cords of communication between the sympathetic and the spinal nerves, consist principally of tubular fibres; but Remak detected in them some grey fasciculi sent from the sympathetic ganglia to the intercostal nerves; so that there is an interchange of filaments in them.

In the difference of microscopic character between the sensitive and motor and the organic fibres, an excellent means is afforded us of ascertaining how far the branches of communication between the cerebro-spinal and ganglionic nerves belong to the one system or to the other. Many nerves, which were formerly regarded as wholly sympathetic, are thus found to be in part of the nature of cerebro-spinal nerves.

While the fibres sent from the otic ganglion to the buccinator nerve are grey, those which come off from the ganglion posteriorly, namely, the nerve of the tensor tympani and the nervus petrosus superficialis minor of Arnold, which goes to join the tympanic plexus, are, on the contrary, more nearly white; the first is indeed perfectly white. Schlemm had pointed out that the nerve of the tensor tympani arises from the third division of the nervus trigeminus, namely, from its pterygoid branch, and I had shown the probability that it is accompanied by fibres from the ganglion. The microscopic examination of the nerve, which I have instituted in the calf, confirms that view. It consists nearly wholly of cylindrical fibres; I could recognise scarcely any grey organic fibres in it. The nervus petrosus superficialis minor I found to consist of a large white fasciculus, and of a bundle of grey fibres which could be easily separated from the former, and which on reaching the tympanum formed a small spindle-shaped ganglion, such as are frequently met with in examining the organic nerves with the microscope. After it had formed the ganglion, the grey thread continued its course with the white portion of the nerve. The latter consisted for the most part of tubular fibres; the grey fasciculus was formed wholly of organic fibres.

The nervus petrosus superficialis major, the superficial branch of the vidian, which runs from the spheno-palatine ganglion to the facial nerve, contains numerous tubular and some organic fibres. The grey fibres, which leave this nerve to join the facial, form in it a small ganglion, from which grey fibres issue, and accompany the latter nerve in its peripheral distribution. From the part of the facial nerve where this ganglion is situated, namely, from its angular bend, a thread is given off, as is well known, to the acoustic nerve.

The tympanic plexus or anastomosis of Jacobson, in the human sub-

ject, is found by microscopic examination to contain tubular fibres and very many organic fibres.

The deep branch of the vidian is perfectly grey, and is composed for the most part of the organic fibres, which predominate in the whole of the carotid plexus, although there also some tubular fibres are mixed with them.

2. *Grey or organic fibres in the ganglionic or sympathetic nerves.*—In the former edition of this work the existence of two kinds of fibres in the sympathetic nerve also could only be shown to be probable, it could not then be satisfactorily proved. It was even then suggested, however, that the ganglia of the sympathetic belong to its organic fibres. Remak has by minute examination been able to distinguish even externally in many parts of the sympathetic nerve grey and white fasciculi; and the microscope has in every instance revealed to him tubular fibres in the latter, and the peculiar organic fibres in the former kind of fasciculi. The results of his long and patient investigation render it very probable also that the organic fibres arise from the globular bodies in the ganglia, and from the caudal prolongations of these bodies; he regards it indeed as a fact, that they do arise thus, for he has very frequently seen coming off from the globules of the ganglia filaments beset with granules similar to those observed on the organic fibres. The white tubular fibres have no intimate connection with the globules of the ganglia, and merely pass between them. They can undergo no multiplication in the ganglia; in the whole of their course in the sympathetic system, as in the cerebro-spinal system, they present no division or anastomosis. The organic fibres on the contrary may, if they take their rise from the caudal processes of the globular bodies of the ganglia, undergo an increase in them; and the greater prevalence of grey fibres in the peripheral portion of the ganglionic system, while the main lateral cords of the sympathetic are more nearly white, is in favour of this view. The ganglia must therefore in fact be regarded as the central organs or brains of the system of organic fibres, while the sensitive and motor fibres of the ganglionic nerves are derived from the brain and spinal cord. From the ganglia arise also the organic fasciculi which accompany the cerebro-spinal nerves; thus the superior cervical ganglion is the radiating point for fasciculi of organic fibres which join the cerebral nerves, and which here and there form secondary ganglia. Although the organic fibres do not take their rise in the brain and spinal cord, yet it is probable that they are connected with the spinal cord through the medium of the communicating branches between the sympathetic and spinal nerves, so as to derive an influence from the central organs of the cerebro-spinal system; for Remak several times succeeded in finding organic fibres in the roots of the spinal nerves generally, as well as in the rami communicantes. What relation the ganglia of the posterior

roots of the spinal nerves bear to the system of organic fibres is still uncertain. From the similarity of their structure to that of other ganglia, it might be supposed that they also serve for the origin of those fibres. This, however, would not explain their constant presence on the posterior roots of the spinal nerves. If, as has been frequently imagined, ganglia have an insulating influence on the fibres which traverse them, considering these fibres in the light of conductors, then the ganglia of the posterior roots of the spinal nerves might have the office of deadening the violence of the impression communicated by sensitive nerves to the spinal marrow, and of thus preventing the excitement of the spinal marrow to the production of reflex motions, which do not take place except when the impression on the sensitive nerve has a certain degree of violence. This would agree too with the indistinctness of the sensations in parts supplied by ganglionic nerves of which the ganglia are more frequent. But all this is a speculation resting on a mere hypothesis.

3. *Functions of the organic fibres.*—With reference to the actions and vital properties of the grey organic fibres, two opinions may be held, of which we will now consider the relative tenability. According to one opinion, the fibres in question together with the globules of the ganglia rule over the involuntary movements; according to another, they preside over nutrition, secretion, and the chemical processes generally. In favour of the first view may be adduced the fact, that the cœliac ganglion has a decided influence on the motions of the intestines; on touching the ganglion with caustic potash, namely, an immediate increased activity and acceleration of the peristaltic motions take place. A similar effect is produced, however, by the application of galvanism to the splanchnic nerve before its entrance into the ganglion. It is possible, indeed, that the ganglia may exert an influence on the motor fibres that pass through them, yet at the same time it must be recollected that the globules of the ganglia are more immediately connected with another set of fibres,—the organic. That an intimate relation does exist between the ganglia and the grey fibres, is rendered probable by the frequent occurrence of small ganglia on fasciculi which are perfectly grey; they are very easily seen, for example, on the grey fasciculi which accompany the first and second divisions of the fifth nerve in the calf. It is probable, therefore, that the function of the ganglionic globules, and that of the organic fibres, are one and the same.

The mere existence of distinct sensitive and motor fibres would, *à priori*, lead us to expect that there should be other special fibres to rule over the vegetative processes of the body. The nerves have a most marked influence on secretions, and, if there were but one kind of nerves for the regulation of the movements and the chemical processes, the

increase of a secretion by nervous influence ought to be always attended with spasm, and spasm with increased secretion; while the two phenomena are often met with separately, just as paralysis of the motor power occurs without loss of sensation, and paralysis of sensation without loss of motion. If, moreover, we consider how frequently the grey fibres join the trigeminus, abducens, and facial nerves, in the first of which they can be traced distinctly in their course towards the mucous membranes of the mouth and nose; if we recollect that in the tympanum there is a plexus, formed principally of organic filaments, destined for the supply of the mucous membrane; and that no involuntary motions are performed by the mucous membranes, or even by the parts to which the second division of the fifth nerve and the nervus abducens are distributed; we shall at once perceive the much greater probability of the second opinion—namely, that the organic fibres in the cerebro-spinal, as well as in the ganglionic nerves, have the function of regulating the organic processes of nutrition and secretion. This view is much favoured, too, by the fact that the sympathetic receives from the motor roots of the spinal nerves motor tubular fibres, on which the involuntary motions must be dependent. If this be really the function of the organic fibres, the motor nerves of the heart ought to consist principally of the white tubular fibres. And such is in fact the case. Microscopic examination of the cardiac nerves of the calf shows them to contain a great number of tubular fibres, which differ from the nervous fibres distributed to voluntary muscles merely in having a smaller diameter; and, if we compare the cardiac nerves with the splanchnic nerves which supply the secreting viscera, the much greater tendency to the formation of ganglia in the latter nerves will strikingly distinguish them from the former. The cardiac nerves develope no central ganglia, the splanchnic swell out to form the great cœliac ganglion. There is the same difference between the nerves of the heart and those of the generative organs supplied from the hypogastric plexus. Those, too, which accompany the renal vessels to the kidneys, are composed in by far the greater part of grey organic fibres. The organic nerves of the penis, which I have described* as entering the corpora cavernosa at their root, and on which erection is dependent, are grey.

In many cases the organic fibres appear to be wholly interwoven with the cerebro-spinal nerves. In this way we might explain the absence of a proper sympathetic nerve in the cyclostomatous fishes (in the petromyzon as well as in the myxinoidea). The nervus intestinalis formed by the two nervi vagi runs, in the myxinoid fishes, along the line of insertion of the mesentery as far as the anus. And on this supposition

* Ueber die organischen Nerven der erectilen männlichen Geschlechts-organe. Abhandl. der Königl. Akad. der Wissensch. zu Berlin, 1835.

only can we explain the fact, that in the human mammary gland there are, according to my observation, no special organic nerves. All the nerves of the glandular substance of the mamma are derived from the third and fourth intercostal nerves.*

CHAPTER V.

OF MOTOR, SENSITIVE, AND ORGANIC NERVES IN THE NERVOUS SYSTEM OF THE INVERTEBRATA.

THE discovery of the sensitive and motor properties of the roots of the spinal and cerebral nerves has enabled physiologists to form better notions concerning the composition of the nervous system of the invertebrata. The observations of Treviranus and myself had shown the presence of a third cord in the nervous system of the scorpion; but I was far from perceiving the importance of this fact. Dr. Grant and Mr. Newport have brought into this field of comparative anatomy the aid of physiology. Professor Grant pointed out that the upper cord of the nervous system of the arachnida, which takes no part in the formation of the ganglia, is analogous to a motor column, and that the lower ganglionated cords are analogous to sensitive columns; the nerves arising from the lower cords he regarded as sensitive nerves, those arising from the upper cord as motor; and he applied this view of the nervous system to the articulata generally.† Still further light has been thrown on this subject by Mr. Newport.‡ He describes the abdominal cord in insects and crustacea to be composed of an anterior and posterior pair of columns. The upper columns do not contribute to the formation of the ganglia, which belong entirely to the inferior columns. According to analogy, the non-ganglionic cords are motor, those on which the ganglia are formed sensitive; but the relative position of the columns is the reverse of what it is in vertebrate animals, in which the ganglionic roots are posterior or superior. Treviranus and Prof. E. Weber had suggested that the ganglia of the abdominal cord of articulata correspond to the ganglia of the posterior roots of the spinal nerves. The mixed nerves which come off from the abdominal nervous cord arise, according to Mr. Newport, in the astacus marinus by roots, which are derived partly from the ganglia, and partly from the upper non-ganglionic columns.§ Other nerves are described by Mr. Newport to arise solely from the upper columns, receiving no root from the ganglia,

* Archiv. für Anat. u. Phys. 1837. Jahresb. xxvii.

† Lancet, July 1834. [Dr. Grant held these opinions at least as early as November 1832, when he taught them in his lectures.]

‡ Philos. Transact. 1834, part 2.

§ [The discovery of the existence of superior non-ganglionic columns distinct from the ganglionic columns in the lobster is claimed both by Dr. Grant and Mr. Newport. See the Lancet for February 17th and March 3rd, 1838.]

and to be distributed solely to muscles; these must certainly be motor nerves.*

Dr. Sharpey has communicated to me a fact, which I mention here on account of its importance. He has observed that the nerves of the arms of the cephalopods (the octopus) have a structure perfectly similar to that of the abdominal cord of the articulata. They consist, namely, of two pairs of cords, of which one pair presents, at points corresponding to the situation of the suckers, ganglionic enlargements, over which the other pair passes without contributing to their formation.

The visceral system of nerves in insects consists, according to M. Brandt,† of three cords, which form ganglia on the œsophagus and stomach; sometimes the lateral cords are imperfectly developed, at other times the middle one. All are connected with the cerebral ganglion (see figs. 44 and 45). They give branches to the mouth, œsophagus, and stomach, and principally to parts of which the movements are involuntary. The lower portion of the intestinal canal does not receive its nerves from this source. Lyonnet and Swammerdam described the commencement of the central visceral nerve, which has since been usually called the nervus recurrens, although Meckel and Treviranus pointed out its analogy to the sympathetic. I described its more developed form in almost all the orders of insects. (Nova Acta, t. xiv.) Brandt's researches have made us still better acquainted with the visceral nerves, not only of insects, but also of crustacea, mollusca, and annelida. From the formation of ganglia in the course of their peripheral distribution, and from their destination for parts endowed

* [In the scolopendra there is a body running down over the dorsal surface of the abdominal nervous cord, which has been described by Dr. Grant as the motor column of this myriapod, (Outlines of Comparative Anatomy, pp. 192 and 198,) and by Mr. Newport as the respiratory column (Phil. Transact. 1834). It has, however, been clearly shown by Mr. Lord to be a part of the vascular system. (See the Medical Gazette for March 3rd, 1838.) The dorsal vessel, or heart, divides, a short distance behind the cerebral ganglion, into two principal branches, which pass one on each side of the œsophagus, and unite below it to form this abdominal vessel. The structure here described is most distinctly seen in Mr. Lord's preparations. Mr. Newport had suspected that this body, and the so-named motor column of the scorpion, were vessels; and, in the Medical Gazette for March 17th, he has confirmed Mr. Lord's description of the vessel in the scolopendra, and states, moreover, that he satisfied himself that the enigmatical column in the scorpion is a similar structure. He calls it the supraspinal vein, and both describes and figures it as giving off numerous branches. The translator still thinks, however, and in this he adopts the present opinion of Mr. Lord, that Prof. Müller was correct when in his original account of this body, which he styled a ligament, he said that it gives off no branches and contains no cavity. Mr. Lord has examined it with the aid of the microscope, and finds it to be a coarse fibrous structure.]

† Mem. de l'Acad. de Petersb. iii.; Ann. d. Sc. Nat. v. 81; and Müller's Archiv. 1836. Jahresb. p. c.

with involuntary motion, it follows that this system of nerves is analogous rather to the sympathetic of vertebrate animals than to the vagus; the fibres corresponding in function to the vagus may, however, be included in it. The principles above stated, relative to the composition of the sympathetic nerve of vertebrata, suggest very different views from those hitherto adopted in the comparison of visceral nerves. Organic fibres may, we now know, be superadded to many and different nerves. As nerves of mixed function, probably containing also organic elements, I regard the interganglionic or transverse nerves of insects, so minutely described by Mr. Newport. The cord from which these nerves arise, and which unites them into a separate system, descends in the middle line, passing over the ganglia. They are distributed principally to the muscles engaged in respiration and to the tracheæ. Since this system of nerves is connected also with those of animal life, it remains uncertain whence the nerves which supply the muscles are derived. If the principles established with regard to the nervous system of vertebrata may be extended to these animals, we should imagine that the branches of communication between the system of interganglionic nerves and the nerves of animal life, are in part destined to convey to the latter nerves organic filaments, or, at least, the peculiar filaments of the interganglionic system.

SECTION III.

Of the mode of propagation of nervous action in the different nerves.

It is yet uncertain whether nervous action, which is propagated with such immeasurable rapidity, be owing to the passage of an imponderable matter along the nerves,—whether the action of a nerve separated from the nervous centres when irritated, is owing to a current of such an imponderable matter taking place through it; or whether nervous action consists merely in oscillations or vibrations excited by the brain or the external stimulus, in an imponderable nervous principle present in the nerves; and it is a problem at present as little capable of solution as the same question with reference to light, namely, whether the theory of emanation or undulation of light be correct. But the decision of this difficulty is no more necessary to the study of the laws of nervous action, than is the knowledge of the true theory of light necessary for ascertaining the laws of its reflection, refraction, &c. The nature of the nervous principle will be considered, however, in the fourth chapter of this section.

In comparing the different parts of the nervous system, we find conductors and excitors of nervous action. The conductors are the nerves; the excitors, the central organs. The nerves, however, have not merely the quality of conductors; for, after separation from the brain,

they are for a certain time capable of exciting, when irritated, contractions of the muscles; but, after they are thus cut off from communication with the central organs, they gradually lose this faculty. Regarding the nerves as conductors, the propagation as well as the action of the nervous principle may be explained by either of the theories above mentioned. Either the imponderable fluid is transmitted in a certain direction through the nerves as a current, or there is merely an oscillation excited in this fluid within the nervous fibres. The rapidity of nervous action again may depend either upon the rapidity of the transmission of the nervous fluid between the brain and the peripheral parts, or on the velocity with which a vibration commencing from the brain, or any given point of a nerve, is propagated to its peripheral extremity, or *vice versâ*.

The attempts made to estimate the velocity of nervous action have not been founded on sound experimental principles. Haller calculated that the nervous fluid moves with the velocity of 9000 feet in a minute; Sauvages estimated the rate of its motion at 32,400: another physiologist, at 57,600 million feet in a second.* Whilst the galvanic principle and the nervous principle were regarded as identical, the rate at which the latter acts was calculated from the rapidity with which electricity is transmitted through conductors. We shall probably never attain the power of measuring the velocity of nervous action; for we have no opportunity of comparing its propagation through immense space, as we have in the case of light. Attention has recently been drawn to the fact, that astronomers have perceived a want of accordance in the observation of very minute intervals of time by the sense of hearing, and of minute divisions of space by the sense of sight; a want of accordance which might incline some to believe that the velocity of nervous action is different in different parts of the nervous system, and even in different individuals. The facts were detailed by M. Nicolai, Director of the Mannheim Observatory, and were communicated by Professor Treviranus to the meeting of naturalists and philosophers at Heidelberg. They are so important that I must transcribe the account of them without abridgment.

"A very large proportion of astronomical observations consist in noting, by means of a second-watch, the moments at which a star, in the daily apparent revolution of the celestial sphere around its axis, passes before the micrometer threads of a fixed telescope. The space which a star traverses in the telescope in the course of an entire second, particularly when the instrument is of high magnifying power, is so considerable, that the moment of the transit of the star before the thread of the micrometer can be indicated to the nicety, not merely of one-half or one-third of a second, but with some practice, and in a favourable state of the atmosphere, even of one-tenth of a second. In

* See Haller's Elementa, t. iv. p. 572.

making these observations, two senses are necessarily engaged simultaneously, namely, sight and hearing. While the constant motion of the star in the telescope is followed with the eye, the ear notes each stroke of the pendulum clock which stands near, marking the seconds. To determine as accurately as is above stated the moment of the actual transit of the star before the micrometer thread, the astronomer, when the star has approached near to the thread, observes the exact distance which it still is from it at the moment of a certain stroke of the pendulum; and likewise the distance to which it has reached on the other side of the thread when the next stroke of the pendulum takes place. From the comparison of the two distances on each side of the thread may be estimated with great accuracy the true moment of the transit of the star past the thread, or the very fraction of the second in which it took place. Several years since, the celebrated Director of the Königsberg Observatory, Professor Bessel, remarked that he evidently did not note the moment at which the star impinged on the threads synchronously with his fellow observers. More particular attention was hereupon paid to this circumstance, and it was made the subject of a more accurate examination in a series of experiments. The result was, that the moments noted by Prof. Bessel always differed from those indicated by others, and the moments noted by his fellow observers again differed more or less from each other; while, in the results obtained by each observer individually, there was not the least discrepancy. I, likewise, says Nicolai, have twice had an opportunity of investigating this point. In the spring of 1827, Prof. Knorre, Director of the Imperial Observatory of Nicolajef, visited me, and we took advantage of his stay in Mannheim to institute some observations together. On an accurate comparison of the results which we obtained individually, it was found that Professor Knorre noted the true moments of the observations as much as half a second later than I did. A few weeks since, I repeated this interesting experiment with another practised observer, already celebrated as the author of several astronomical and mathematical papers, M. Thomas Clausen, from Denmark. He noted the moments in each observation about one-third of a second later than I did. Between other observers the difference is even much greater; thus, between Professors Bessel and Knorre it reaches the extraordinary extent of a whole second; Professor Bessel noting his observations as much as a second earlier than Professor Knorre. This remarkable circumstance has been subjected to so many tests by several observers that the fact is placed beyond all doubt."*

M. Nicolai maintains that the above remarkable fact cannot be explained except on the supposition of a difference in the rapidity of transmission from the eye to the sensorium, and from the ear thither. If we admit, namely, that the one individual, in directing both these

* Isis, 1830, p. 678.

senses to the same object, sees sooner than he hears, and that in the other individual the impressions are conveyed to the brain more nearly or quite simultaneously, or even in the reverse order,—hearing in him taking place sooner than sight,—the phenomenon will be completely and without difficulty explained; but such an explanation involves the important assumption, that the reciprocal action between the organs of sense and the brain is not perfectly momentary. The above phenomena would indeed afford a hope that the problem of the velocity of nervous action is nearer solution, were it not that they may be explained in another and more probable manner. It is well known that the sensorium does not readily perceive with equal distinctness two different impressions; and that, when several impressions are made on the nerves at the same time, the sensorium takes cognisance of but one only, or perceives them in succession. When, therefore, both hearing and sight are directed simultaneously to one object, this will necessarily be first heard, then seen. The interval of time, however, between the two perceptions by the sensorium is greater in some individuals than in others: some persons can receive and be conscious of many impressions at the same moment, for which others require a considerable interval.

The time required for the propagation of a sensation from the surface to the brain and spinal marrow, and for the reflected action producing contractions of the muscles, is immeasurably short. Frogs poisoned with opium or nux vomica are, at first, in a state of such excessive sensibility, that the slightest touch on the skin excites convulsions of the whole body. Here the impression made on the skin is propagated first to the spinal cord, and from the cord to all the muscles; and, nevertheless, I have been unable to detect the slightest interval between the moment when the skin was touched and the occurrence of the muscular spasms.

CHAPTER I.

OF THE LAWS OF THE ACTION OF MOTOR NERVES.

a. Of the laws of the transmission of nervous influence in motor nerves.

I. *The motor influence is propagated only in the direction of the nervous fibres going to the muscles, or in the direction of the ramification of the nerve; never in a retrograde course.*—It is a fact generally known, that by irritation of a motor nerve, contractions are excited in no other muscles than those to which the nerve distributes branches. When a nerve is irritated, either by chemical, mechanical, or electric stimuli, or by the application of both poles of a galvanic circle to the nerve itself, all the muscles supplied by the branches given off by the nerve below the point irritated are thrown into contractions, and those muscles only. The muscles supplied by the branches which come off from the nerve at a

higher point than that to which the stimuli are applied, are never excited to contractions. Not the slightest twitchings are ever produced in the muscles of the thigh by irritating the lower part of the ischiadic nerve.

II. *The application of mechanical or galvanic irritation to a part of the fibres of a nerve does not affect the motor power of the whole trunk, but only that of the portion insulated from the rest, to which the stimulus is applied.*—This experiment can be best performed on rabbits, on account of the larger size of the nerves in them than in frogs. The ischiadic nerve being laid bare where it issues from the pelvis, different portions of it, which afterwards separate from the trunk as branches, may be easily irritated individually with a needle; and it will be satisfactorily seen, that those muscles only are thrown into contractions to which the irritated portion is ultimately distributed. To be able to see the slightest twitchings of the muscles, the skin must be removed from the whole limb as far as the foot. Having separated the ischiadic nerve, before its division into the tibial and peroneal nerves, into several bundles, I irritated each of these singly, and saw different muscles thrown into contraction by the irritation of different nervous fasciculi; thus, according to the fasciculus of the nerve that was irritated, the effect produced was contraction of the muscles of the calf, or extension or flexion of the toes. By separating the nervous fasciculi in the peroneal nerve, and irritating them singly, I was even able to cause contractions of different parts of the muscles of the calf of the leg. The same experiment may be performed with galvanism, the two poles of the circle being applied directly to a bundle of fibres carefully separated, without stretching, from the ischiadic nerve in a frog. If, however, both poles are not applied directly to the separated fibres, but one to them, and the other to the trunk of the nerve, contraction, not of one muscle, or set of muscles only, but of the whole limb, will ensue;* for in this case the galvanic stimulus is not confined to a few fibres, but is conducted to the trunk of the nerve, and the effect is the same as if both poles had been applied immediately to the entire nerve.

III. *A spinal nerve entering a plexus, and contributing with other nerves to the formation of a great nervous trunk, does not impart its motor power to the whole trunk, but only to the fibres which form its continuation in the branches of that trunk.*—This is shown by experiments of Van Deen, myself, and Kronenberg.

In the frog, the three nerves which go to form the ischiadic plexus may be irritated singly before their union. I found that irritation of the first produced twitchings of the muscles of the inner side of the thigh; irritation of the second, which with the third forms the ischiadic nerve, gave rise to contractions of the muscles of the thigh and leg, not

* Humboldt, loc. cit. i. p. 212.

of the foot (the foot also was somewhat affected in Kronenberg's experiments); and when the third nerve was irritated, motions of the thigh, leg, and foot ensued. Van Deen's experiments were instituted in a different manner. He divided singly each of the nerves forming the plexus, and found that, although they were all connected together, yet different muscles were paralysed. The first forms the inguinal nerve; and is connected by a short communicating branch with the second nerve, this communicating branch being generally derived from the second nerve and added to the first, though occasionally it is formed by a part of the first given off to the second nerve: when now he divided this inguinal nerve, the frog continued to exercise all the motions of the limb, except that of drawing the thigh towards the trunk. Division of the second nerve before its entrance into the plexus put a stop to all motions of the muscles of the thigh and leg, while the motions of the foot were performed as before. Division of the ramus communicans between the inguinal nerve and the second nerve of the plexus, deprived the frog of the power of raising the limb towards the abdomen; the same was the result of division of the inguinal nerve after this communicating branch had joined it. By dividing the ischiadic nerve longitudinally from the point of union of its two roots, the same effect was produced as by transverse division of the entire trunk of the nerve,—namely, paralysis of the thigh, leg, and foot; whence Van Deen infers that the fibres of the two roots decussate at their point of junction. Division of the third nerve (the second root of the nervus ischiadicus) paralysed the foot, and in a great degree the leg.

The experiments of Kronenberg * differ in some particulars from the foregoing, but they lead to the same results; as do those also which he performed on the nerves that form the brachial plexus. He proves, in a very ingenious manner, that the motor power is not communicated from one fibre to another in their course in a nerve, that no such effect as this results from the constant interlacement of the nervous fibres. He nearly divided a nerve in a frog, leaving only a small portion uncut at one border; and at a little distance below this he made another similar incision, but on the opposite side of the nerve. He now irritated the nerve above the upper incision, but could excite no action of the nerve and muscles below the second incision. The plexuses of nerves seem to be destined, as far as their motor power is concerned, to convey to each muscle fibres from different parts of the brain and spinal cord. This is effected by the plexus brachialis, for example, as its minute dissection shows. The plexuses may also be intended to intermingle the sensitive and motor fibres, in accordance with the wants of the parts to which the nerves are distributed.

The foregoing results of experiments prove that the individual fasciculi of primitive fibres which go to form a nervous trunk, exercise their

* Plexuum nervorum structura et virtutes. Berol. 1836.

motor power in that trunk in an insulated manner, without exciting to action the other primitive fibres of the nerve. But even single portions of a muscle may contract separately; for example, the separate portions of the flexores communes, and of the extensor communis digitorum for the individual fingers. The gluteus medius has perfectly different actions, according as its anterior or its posterior portion contracts. The first rotates the thigh inwards, the latter outwards. The different parts of the sphincter palpebrarum, and of the sphincter oris, can act separately. This must depend on the action of different nervous fibres.

Facts are every day observed which confirm the above remarks, and show that, although the same nerves frequently give branches to many different muscles, the cerebral influence can nevertheless be limited to particular branches or single fasciculi of a nervous trunk. The nervous influence transmitted from the brain, for example, in diseases of that organ, is frequently confined to most minute portions of muscles, which then are affected with tremors. Moreover, we know that the primitive fibres of nerves are anatomically distinct; so that taking into consideration both the anatomical and physiological facts, we are justified in the conclusion that even the individual primitive fibres in the nerves and their branches maintain their motor power insulated within themselves. At the period when the principle of which the effects were seen in the galvanic experiments on animals, and which was then called animal electricity, was regarded as the cause of nervous power, this latter power must have been supposed to act at a certain distance. The galvanic phenomena produced in animals by the influence of metals, suggested to Humboldt and Reil the idea of the sensible atmosphere of the nerves. Humboldt was the first to discover that two metals produce the usual effects, even when held at the distance of five-fourths of a line from the muscle or the nerve. He also observed that this galvanic current was in this case conducted by imperceptible vapour of fluids, for the effect ceased as soon as the evaporation was prevented, while the galvanism acted more powerfully in proportion to the facility and rapidity with which the fluid employed evaporated; the mere breathing on dry metallic plates which had ceased to excite reaction of the muscles, restored their galvanic power.

b. Of the associate or consensual movements.

I here refer to those movements which, contrary to our will, accompany other, voluntary, motions. Several of these phenomena were formerly confounded with others of a different nature. Examples of the true consensual movements are very frequent, even in the healthy state of the body. When we endeavour to contract the muscles of the external ear, we induce motion of the occipito-frontalis muscle also, and of several muscles of the face. When we wish to elevate and depress the

alæ nasi, we corrugate at the same time, without willing it, the eyebrows. Very few persons indeed can cause the different muscles of the face to act singly; they cannot in most instances make the individual muscles act, except in groups with other muscles. The perineal muscles, the sphincter ani, levator ani, transversus perinæi, accelerator urinæ, and compressor urethræ, nearly always act simultaneously when the volition is directed to one only. This association of movements is most striking in the case of the iris. We cannot move the eye inwards by the action of the rectus internus, without contraction of the iris being produced. The iris contracts likewise whenever the eye is turned upwards and inwards by the action of the obliquus inferior. The motor influence both for the two muscles here named and for the iris is derived from the same nerve, namely, the nervus motorius oculi, which supplies the short motor root to the ciliary ganglion. When, therefore, the influence of volition is directed upon the motorius oculi nerve, or rather upon those of its fibres which supply the muscles in question, the nervous stimulus is always communicated in a certain degree to other primitive fibres of the nerve,—to those, namely, which form the short root of the ciliary ganglion.

Similar phenomena are indeed observed in all parts of the body. Most persons find a difficulty in calling into action separately the individual portions of the musculus extensor com. digitorum, so as to extend singly separate fingers; for example, the third or fourth, which have no special extensor muscles. During violent bodily exertion many muscles act by association, although their action serves no apparent purpose; a man using great muscular exertion moves the muscles of his face, as if they were aiding him in raising his load; during laboured respiration, and in persons in a state of debility, the muscles of the face act simultaneously but involuntarily; although, except by raising the alæ nasi, they can in no way assist respiration. The phenomena of this kind are so numerous, so frequent, and so constantly the same, that the few examples which we have cited will be sufficient. I must, however, mention one fact as worthy of special attention, since it is the most complete example of the tendency to consent of muscular action between similar parts of the right and left side of the body. It is the involuntary motion of the iris. The motion of the iris is always simultaneous in the two eyes, as well when it is excited by an external stimulus, as when it is the effect of volition; even when the stimulus, be it external or internal, acts on one eye only, both irides contract equally. If but one eye be opened, the contraction of the pupils will be less than when an equal impression of light falls upon both eyes. If the impression of light on the two eyes be unequal, the size of the pupil in the two will still be equal, but it will be the mean between those which the two different impressions of light would produce. The same law prevails when

the motions of the iris are determined by internal volition. We can at any time voluntarily excite consensual motion of the iris, as I have already stated, by rotating the eye inwards, or inwards and upwards; but the most remarkable circumstance is, that the iris of both eyes contracts when one eye only is turned inwards, the other being still directed forwards. The power which every one has of contracting the iris by turning inwards the eye, I possess in an extraordinary degree. If I cover one eye, A, and look directly forwards with the other eye, B, I can move the iris of this eye, which I keep fixed, at will, contracting it or dilating it according as I rotate the covered eye, A, inwards or outwards. In this experiment, the cause of the motion of the iris is concealed, and the motions are the more striking from the eye in which it is seen to take place being fixed. The cause, however, is immediately evident when I open the eye, A; it is then perceived that to produce a contraction of the iris in the fixed unmoved eye, B, I always rotate inwards the other eye, A. It is obvious that there must be a certain arrangement of the fibres in the brain, which gives rise to the tendency to association in action of those fibres of the two motores oculi which go to form the ciliary nerves. An interesting fact, easily explicable according to the principles here laid down, is the contracted state of both irides in sleep. It is a consensual motion dependent on the position of the eyes, which are turned upwards and inwards by the inferior oblique muscles. Many other muscles of the two sides of the body, besides the irides, have a tendency to association in their movements. Thus the muscles of the eyes have this tendency; it is impossible, for example, to turn one eye downwards, the other outwards, or both outwards at the same time. When one eye is turned outwards, the other is always rotated involuntarily inwards.* It requires practice to be able to keep one eye open while the other is shut; that is to say, to contract the levator palpebræ of one side only by the influence of the motor-oculi nerve. Few persons have the power of moving, by the influence of the facial nerve, the muscles of one side of the face differently from those of the other side. I can move the muscles of the ear, even the smaller ear-muscles, the anti-tragicus at least, quite distinctly; but when I determine voluntarily these motions in one ear, they always take place on the other side also. I do not know whether it be possible to cause the musculus stylo-hyoideus of one side to contract alone. There is a similar tendency to consentaneous motion between the corresponding muscles of the two sides of the trunk, but it is much less marked: the abdominal and perineal muscles, and the diaphragm, nearly constantly act simultaneously on the two sides; and even the nerves and muscles of the extremities, although they are more independent in this

* This phenomenon will come under consideration in the second section of the 4th book, on muscular motions.

respect, are not wholly exempt from the general law. The difficulty of executing simultaneously with the two upper or the two lower extremities, rotatory motions in opposite directions, for example, around a common axis, is well known; while similar motions with both extremities are much more easily performed.

The explanation of all these phenomena is evident. The primitive fibres of all the voluntary nerves being at their central extremity all spread out in the brain to receive the influence of the will, we may compare them, as they lie side by side in the organ of the mind, to the keys of a piano, on which our thoughts play or strike, and thus give rise to currents or vibrations of the nervous principle in a certain number of primitive nervous fibres, and consequently to motions. From the conducting power of the cerebral substance at the origin of the nervous fibres, however, those which are contiguous to each other must be liable to be affected simultaneously, and the influence of volition will with difficulty be confined to single fibres. By repeated exercise, this faculty of insulating the influence of the will is acquired; that is to say, the more frequently a certain number of nervous fibres are exposed to that influence, the more prone do they become to obey it independently of other surrounding fibres; or, in other words, certain paths for the more ready transmission of the cerebral influence are gradually developed. This faculty of insulation of the influence of volition is seen to reach the highest degree of perfection in certain arts, for example, in the use of musical instruments, particularly of the piano.

All associate movements have their source in the brain itself; they cannot be attributed to a communication between the primitive fibres in the motor nerves; for, in the first place, the primitive fibres do not communicate with each other; and, secondly, irritation of a portion only of a great nervous trunk never influences the rest of the nerve, but is propagated only to those branches of it which are formed of the fibres irritated. (See page 681.)

The associate movements cannot, moreover, be ascribed to the action of the sympathetic nerve, which maintains communications neither between different portions of a motor nerve, nor between the corresponding nerves of the two sides of the body; such communications are effected solely by the brain and spinal cord.

CHAPTER II.

OF THE LAWS OF THE ACTION OF SENSITIVE NERVES.

a. Of the laws of the propagation of the nervous influence in the sensitive nerves.

A NERVE preserves its sensitive power only so long as it maintains its communication with the sensorium, either directly, or indirectly through

the medium of the spinal cord. We will now consider here, as in the case of the motor nerves, the relation which exists between the trunks and branches.

I. *When the trunk of a nerve is irritated the sensation is felt in all the parts which receive branches from it; the effect is the same as if all the ultimate ramuscules had been irritated.*—If one branch only of a nerve be irritated, the sensation produced is confined to the part to which that branch is distributed; if the irritation be applied to the trunk itself, the sensation is felt in all the parts to which the nerve sends branches. These experiments can of course be instituted only in one's own person; but the results they afford are as certain as those of the experiments on motor nerves in animals. If we stretch or pinch the ulnar nerve intentionally, by pushing it from side to side, or compressing it with the fingers, where it lies at the inner side of the elbow-joint above the internal condyle, we have the sensation of "pins and needles," or of a shock, in all the parts to which its ultimate ramuscules are distributed, particularly in the palm and back of the hand, and in the fourth and fifth finger. If stronger pressure be made, the sensations are felt in the fore-arm also. By drawing the thumb up and down, at the same time exerting pressure along the inner side of the upper arm, and by pressing deeply quite at the upper part of the arm at the inner side, we may easily reach the median and radial nerves, and excite similar sensations in the parts to which they are distributed. Pressure on the main nervous trunk of a limb—for example, on the nervus ischiadicus,—produces the well-known sensation of pins and needles in the whole limb, or that of the limb being "asleep." By a particular position of the thigh in the sitting posture, the ischiadic nerve may be compressed at its very exit from the pelvis. Having ascertained the situations where other, even small nerves, can be subjected to such mechanical irritation, we may in this way institute experiments in our own person analogous to those performed on animals with reference to the motor function.

II. *The sensation produced by irritation of a branch of a nerve is confined to the parts to which that branch is distributed, and, generally at least, does not affect the branches which come off from the nerve higher up, or from the same plexus.*—The facts by which this is proved are so well known that it is unnecessary to detail them singly. Irritation of the skin is ordinarily felt only in the spot where the irritant is applied. The irritation never reacts upon the brachial plexus for example, and on the other nerves which arise from it. Gaedechen has already shown,* that a sensation excited in one sensitive nerve is not transmitted to another sensitive cerebro-spinal nerve with the branches of which the first communicates; but that the anastomosis of the nerves is merely a means for the more extended distribution of the primitive fibres in the peripheral

* See the account of experiments on the facial and infra-orbital nerves, at page 658.

direction. Gaedechen's experiments prove that, in the anastomoses between the facial and infra-orbital nerves, the fibres of the one nerve are never reflected backwards on the trunk of the other; but that the fibres of both, though mingled with each other, still follow their peripheral course. The same law prevails here, therefore, as in the case of motor nerves, in which the irritation of one branch never excites contractions in the parts supplied by others which come off from the nervous trunk higher up. Under certain conditions, however, the irritation of a single nerve will give rise to sensations over a very great extent of the body. Such phenomena, however, are owing to a particular action of the brain and spinal marrow, and not to the reciprocal action between the nerves themselves.

III. *When, in a part of the body which receives two nerves of similar function, one is paralysed, the other is inadequate to maintain the sensibility of the entire part; on the contrary, the extent to which the sensibility is preserved corresponds to the number of the primitive fibres unaffected by the lesion.*—When two nerves anastomose, they have not the power of compensating for the inactivity of each other, as is the case when two arteries anastomose; wherever two cerebro-spinal nerves unite to form a thicker trunk, the paralysis of one root of this trunk deprives of their power all the primitive fibres derived from that root. Thus, when the ulnar nerve, which supplies the fourth and fifth fingers, and a part of the third, is divided, the sensibility of those parts is not supplied through the medium of the anastomosis of the ulnar with the median nerve: the fourth and fifth fingers are permanently deprived of sensibility. If the outer side of the fourth finger retains a slight degree of sensibility, it must be due to the primitive fibres of the median nerve which join the volar branch of the ulnar. The slight sensibility which remains in a member after its nerve is paralysed can, therefore, always be accounted for by the circumstance of the nerve being joined by fibres from other nerves, though there is no real coalescence or communication between these fibres and its own elements. These principles are illustrated by the history of local paralyses. In a case in which Mr. Earle* cut out a portion of the ulnar nerve behind the internal condyle of the os humeri, the little finger, after the lapse of five years, was still nearly useless, and its sensibility imperfect. With reference to this case, Mr. Swan† with justice asks, "If the supposed communication existed even in a small degree, would not the anastomoses between the portion of the ulnar nerve below the division, and the median, spiral, and internal cutaneous nerves, have kept up a sufficient communication with the brain, had the transmission of the nervous influence been easy?"

Mr. Swan relates another case, in which an incised wound was received

* Medico-Chirurg. Transact. vol. vii.

† Local Morbid Affections of the Nerves, p. 63.

in the fore-arm three inches from the wrist-joint, apparently dividing the median and radial nerves; and here the thumb and two contiguous fingers, with the corresponding parts of the hand, lost their sensibility; while the fourth and fifth fingers, and the parts of the hand to which the ulnar nerve is distributed, remained sensible.

In the numerous anastomoses, therefore, which nerves appear to form, and in the anastomoses which the sheaths of the fasciculi of the same nerve form at every inch of its course, while the primitive fibres are continued onwards without uniting, there is nothing analogous to the anastomoses of arteries, but merely a provision for supplying the same parts with fibres from different nerves; of which arrangement one great advantage is, that injury of one nerve does not wholly cut off the part to which it is distributed from communication with the brain.

IV. *When different parts of the thickness of the same nerve are separately subjected to irritation, the same sensations are produced as if the different terminal branches of these parts of the nerve had been irritated.*—If the ulnar nerve be irritated mechanically in the manner already described, particularly by pressing it from side to side with the finger, the sensation of pins and needles is produced in the palm and back of the hand, and in the fourth and fifth finger. But, according as the pressure is varied, the pricking sensation is felt by turns in the fourth finger, in the fifth, in the palm of the hand, or in the back of the hand; and, both on the palm and on the back of the hand, the situation of the pricking sensation is different according as the pressure on the nerve is varied, that is to say, according as different fibres or fasciculi of fibres are more pressed upon than others. The same will be found to be the case in irritating the nerve in the upper arm; but the pressure on different parts of the trunk can be made best in the ulnar nerve, it being at one time compressed, at another time pushed from side to side in the hollow between the inner condyle and olecranon by the finger of the other hand. The infra-orbital nerve, likewise, may be pressed upon at its point of exit from the foramen, so as to give rise to a pricking sensation in the cheek and upper lip, the situation of which will vary according as the nerve is alternately pressed directly against the bone, or from side to side. It is much more difficult, however, to perform the experiment on this nerve, since its point of exit from the bone must first be ascertained by means of pressure and the consequent sensations.

V. *The sensations excited in the minute elementary fibres are transmitted from the surface to the brain without being communicated to the other fibrils of the same nervous trunk.*—This is a necessary inference from the facts and laws already detailed. We have shown that the primitive fibres of nerves never either divide or anastomose; that the trunk of a nerve is as it were the aggregate of all the primitive fibres which are developed in its branches; and thus that there is a uniform relation between the fibres of

the stem and the elements of its smallest branches. It has, moreover, been shown that irritation of the trunks of nerves excites sensations in all their branches, but that irritation of one branch of a nerve gives rise to no sensation in the other branches; and, lastly, that irritation of a portion of the trunk of a nerve gives rise to the same sensations as when particular portions of the branches of the nerve, or the parts to which they are distributed, are irritated. When these facts are considered in connection with each other, they force us to the conclusion stated at the head of the paragraph, although they do not prove it strictly with respect to the individual primitive fibres. Prof. E. H. Weber has pointed out that the power of distinguishing the distance between two bodies touching the skin, is very different at different parts of the surface; that at several points,—for example, at the point of the tongue,—the distance of two-thirds of a line between two bodies can be distinguished; while in other parts, as the middle line of the back, the bodies must be separate as much as thirty lines; but this is no proof of the incorrectness of the above conclusion, for this discriminating power of the skin depends on the number of primitive sensitive fibres distributed to a certain extent of its surface.

Another question now suggests itself; namely, when the primitive fibres are irritated at different parts of their course, as in the trunk of a nerve, or in its branches, is the seat of the sensation always the same, or is it felt at different points, so that, from the feeling produced, it can be determined at what point a certain fasciculus of primitive fibres has been irritated, whether in the trunk of the nerve, in the branches, or in the skin, where the fibres are expanded? The answer is, in part, to be found in facts already detailed.

a. Irritation of the trunk of a nerve produces the same sensation as if all the primitive fibres distributed to the peripheral parts were irritated; and the sensation is felt in those peripheral parts, just as if the irritation had been there applied to the fibres.

b. When different primitive fibres composing a nerve are irritated separately, the sensations are felt in different points of the periphery of the body.

c. Irritation of the branch of the nerve is attended with sensation in the parts to which the branch is distributed.

It would appear, therefore, to be a matter of indifference whether the stimulus be applied to the primitive fibres, where they are assembled in the nervous trunk; in the branches, where they are distributed in fasciculi; or in the peripheral parts, where they are isolated from each other. The same sensations as are produced by pricking the skin with needles, or by the creeping of ants over it, are also excited by exerting pressure on the primitive fibres where they lie aggregated in a small twig of a nerve going to a finger, in which case the sensations are confined to the

skin of the finger; or by pressure on the trunk of the nerve, when they are felt in the skin of all the parts which the nerve supplies. If the pressure on the nerve is sudden and violent, the sensation of an electric shock is felt in all the fibres of the nerve; not in the trunk, at the point at which the pressure is made, but in the parts in which the primitive fibres terminate. Similar phenomena are observed when nerves are divided in amputations. At the moment of the division of the nerves, the most violent pains are felt, as if in the part which is being amputated, and to which the divided nerves are distributed. The experienced surgeon of the Hamburgh hospital, Dr. Fricke, assures me that this is a constant phenomenon.

Since each primitive fibre, in its whole length, from the brain to the skin, is in connection with the brain by one point only, namely, by its extremity, it would be expected that at whatever part it is affected, whether at its peripheral extremity, in the middle of its course, or in the nervous trunk, the same sensation must be produced; for all the impressions made upon the primitive fibre, in its whole length, can be communicated but to one point of the brain. The primitive fibres of a nerve, whether long or short, would appear, therefore, to represent each but one point in the brain which makes us conscious of the same sensation at whatever part of its course the primitive fibre may have been irritated. The reason why the sensation appears to have its seat always in the skin, at whatever point of their length the nervous fibres are irritated, seems to be, that the sensations are ordinarily produced by an action on the skin, or on the cutaneous extremities of the fibres. Although these are just conclusions from the observations we have detailed, still, the following facts show that the theory of sensations here given is far from being completely established.

VI. *Although pressure on a nerve gives rise to sensations which are felt in the peripheral parts, yet a stronger pressure produces pain in the nerve itself at the point to which it is applied.*—We experience this but rarely, as when we suffer violent blows on the ulnar nerve. But the experiment may be made by pressing the ulnar nerve with gradually increased force against the bone above the internal condyle, when, in addition to the sensations excited in the parts which the nerve supplies, a pain will be produced at the seat of the pressure; not merely in the surrounding parts, but in the nerve itself. From the facts already detailed, and others that follow, this would not be expected; and there seems to be something here with which we are unacquainted, but which is important with relation to the theory of sensation. Something similar is observed in the case of the tumours of nerves, of which the characteristic symptoms are pains in all parts which the nerve supplies; and violent pains in all those parts attend the division of the nerve above the tumour, as I observed on the occasion of the division of the ulnar nerve in the upper

arm, above such a tumour, by Prof. Wutzer.* But the ganglion, or tumour, of the nerve is itself frequently sensitive and very painful. In cases of disease of the spinal cord, likewise, the pains are commonly felt in all the peripheral parts which lie below the point affected; but sometimes, though rarely, as in neuralgia dorsalis, there is pain along the middle line of the back.

It is to be lamented that operating surgeons have hitherto neglected the excellent opportunities they enjoy of observing the phenomena which attend the division of nerves.

The direction which the pain takes in cases of neuralgia, namely, along the course of the nerves, appears, likewise, not to agree with the theory of sensations above proposed. It must, however, be remarked that neuralgic pains by no means constantly follow the course of the nerves. I have examined several cases of true neuralgia in Berlin, in which the pain did not pursue the course of the anatomical distribution of the nerves.

The following facts are favourable to our theory; we are in want of information calculated to elucidate these apparent contradictions.

VII. *When the extreme parts are completely deprived of sensibility by pressure on a nerve, or by its division, irritation of the portion of the nerve connected with the brain still excites sensations which are felt as if in the parts to which the peripheral extremities of the nerve are distributed.*—Thus there are cases of paralysis in which the limbs are totally insensible to external stimuli; and in which, nevertheless, the paralysed parts are the seat of most violent pain. In the case of a man named Heidenreich, whom I saw at Bonn, and in whom the lower extremities had completely lost both sensation and motion, there were occasionally spasms of the limbs, attended with violent pains in the whole leg, but the sensibility to external stimuli did not return. When the extreme portions of nerves are paralysed, irritation of their trunks may give rise to violent pains, which will be felt in the peripheral parts. It will be at once perceived that the cases in which this occurs must be principally those in which the trunks and origin of the nerves have remained sound,—cases of local paralysis, therefore, where the brain and spinal cord are free from disease; for example, the cases of paralysis from rheumatic and gouty affections, or those from pressure on the nerves, or tumours of them. In a case, related by Mr. Earle,† of paralysis of the arm, consequent on fracture of the clavicle, the fingers and whole arm were insensible to external impressions; and, nevertheless, in every attempt to move the limb, and occasionally even when it was quite at rest, the patient experienced severe pain in the tips of the fingers.

The innumerable cases showing that division of the nerve for neuralgic pain is generally attended with an unfavourable result, and that the

* Compare the observations of Aronsohn, Observ. sur les tumeurs developpées dans les Nerfs. Strasb. 1822, p. 9.

† Med. Chir. Transact. vol. vii. p. 173.

pains frequently return with as great violence as before, although the nerves be divided, and even portions of them removed, afford another confirmation of the above statement. In fact, when the cause of the neuralgia is seated in the trunk of the nerve,—for example, of the facial or infra-orbital nerve,—division of it can be of no service; for the stump remaining in connection with the brain, and containing in itself all the primitive fibres distributed in the branches of the nerve to the skin, gives rise, as we know, when irritated, to the same sensations as are felt when the peripheral parts themselves are affected. It is rarely that division of the nerve, or removal of a part of it, relieves the neuralgic pain; such a result can occur only when the cause of the disease is seated in the branches, not in the trunk of the nerve.

Division of a nerve, then, merely prevents the possibility of external impressions on the cutaneous extremity of the nervous fibres being felt; the impressions being no longer communicated to the brain. But the same sensations which were before produced by external impressions may arise from internal causes, as long as the primitive fibres of the trunk remain in connection with the brain or spinal cord.

When a nerve—of a finger, for example—is accidentally divided, the paralysed portion of the finger, although insensible to external stimuli, becomes, during the existence of inflammation in the wound, the seat of pain. When the inflammation has subsided, the sense of pain ceases, and the part is quite devoid of sensation. The observation of Gruithuisen with respect to these phenomena in his own person, which were related at page 423, are particularly interesting. Sir Everard Home * relates a case in which a nerve of the face was divided for neuralgia, and the wound not uniting by the first intention, the inflammatory state of the divided extremities of the nerve, gave rise to attacks similar to those suffered before the operation; but, when the wound had completely healed, there was no return of the pain.

The phenomena attending the state of a limb "asleep," in consequence of pressure on the nerves, are of similar kind. The pressure puts a stop to the nervous communication from the periphery to the brain; but the same pressure, by affecting the upper part of the nerve, gives rise to the sensation of "creeping" ("formicatio") and pricking in the limb, which has nevertheless lost its sensibility to external impressions.

The sensation of creeping in the surface frequently attends affections even of the origins of the nerves from the spinal cord or brain, or of these latter organs themselves. When the sensation of tingling is felt in the skin, it is impossible to know whether the cause of it be seated in the skin, in the nerves themselves, or at the origin of their fibres from the spinal cord. Its seat is frequently the spinal cord itself. In nearly all diseases of the spinal cord, tingling in the skin is a symptom; the tingling is

* Philos. Transact.

also frequently felt in the paralysed parts which receive their nerves from the cord below the seat of the disease; in tabes dorsalis there is this formicatio or tingling, not merely in the mesial line of the back, but in the skin of the whole, or lower part of the body.

From the foregoing remarks it will be conceived that the aura epileptica, (a kind of "formicatio,") which is felt in the extreme parts of the body before an attack of epilepsy, has its cause and true seat, not in those parts, but in the spinal marrow or brain. It is the first symptom of the affections of the spinal marrow and brain which show themselves during the attack. Should an epileptic fit be occasionally arrested by the application of a ligature to the limb above the seat of the aura epileptica, it must be owing, not to the ligature preventing the transmission of any morbid matter, but to its producing a strong impression on the sensorium. It must be remarked, however, that in the form of epilepsy which is dependent on tumours of the nerves, a ligature applied to the limb really arrests the propagation of the irritation to the spinal cord.

If a tourniquet is applied to the arm above the elbow joint, the first effect is the sensation of pins and needles in all parts of the hand, then gradually numbness and the sensation of cold ensue, and at last insensibility to external stimuli. If now the nerves in the axilla and arm, above the tourniquet, are irritated mechanically by means of the fingers, the sensation of an electric shock will be felt in the hand as distinctly as when the nerves of the fore-arm and hand are not paralysed by pressure.

VII. *When a limb has been removed by amputation, the remaining portion of the nerve which ramified in it may still be the seat of sensations, which are referred to the lost part.*—This is a fact known to all surgeons, and is subject to no exception. It is usually said that the illusion continues for some time, namely, as long as the patient is under the care of the surgeon; but the truth is, that in most cases it persists throughout life: of this it is easy to convince one's self by questioning a person whose limb has been amputated, at any period after the operation. The sensations are most vivid while the surface of the stump and the divided nerves are the seat of inflammation, and the patient then complains of severe pain felt as if in the whole limb which has been removed. When the stump is healed, the sensations which we are accustomed to have in a sound limb are still felt; and frequently throughout life there is a tingling, and often pain, felt, which are referred to the parts that are lost. These sensations are not of an undefined character; the pains and tingling are distinctly referred to single toes, to the sole of the foot, to the dorsum of the foot, to the skin, &c. It is ridiculous to attribute these important phenomena to the action of the imagination, &c. They have been treated merely as a curiosity; but I have convinced myself of their constancy—of their continuance throughout life—although patients become so accustomed to the sensations that they cease to remark them. The sense of tingling

or creeping of ants in the hand, foot, or whole extremity, with the same distinctness as when the limb is still present, may be excited much more vividly by applying a ligature or tourniquet to the stump, or by exerting pressure on its nerve; hence patients have the feeling of their lost limb most distinctly, when from any cause the application of the tourniquet is again necessary. If the patient have suffered before amputation from a local painful affection of the limb, the whole limb will still be felt as if in pain after its removal; and pain is felt as if in the whole limb, at the moment when the nerve is divided, and during the inflammation of the stump.*

* The following are examples of these phenomena:—

a. A woman who had lost the sensibility of one arm had the same limb fractured; mortification ensued in it, and it was amputated in the surgical clinical ward at Bonn. The amputation was not felt; but the division of the nerve must have excited its sensitive power, for in the same night the woman complained of pains, felt as if in the fingers.

b. Joh. Wolff, a journeyman tailor in Bonn, had his leg amputated at the first third of the thigh, twelve years ago. Immediately after the operation his sensations were those of his limb being still present; and, on the following day, he complained much of pains in the leg, extending to the toes. On the same day the arm was removed in another patient, and he likewise complained afterwards of pains in the hand and whole arm. Wolff I found, after the expiration of twelve years, to have still feelings which seemed to be in the toes and sole of the lost foot, and occasionally severe pains referrible to the sole. Sometimes, from pressure in lying, the stump has the sensation of being asleep; and then, as well as frequently at other times, he feels a tingling as if in the toes. I applied a tourniquet to the stump, so as to press upon the ischiadic nerve; and Wolff immediately said that he felt his leg asleep, and a very distinct tingling in the toes.

c. A student in surgery, a Jew, had his arm amputated above the elbow, on account of disease of the joint. As long as we had an opportunity of observing him, he could still feel the lost arm.

d. A student named Schmidts, from Aix, had his arm amputated above the elbow, thirteen years ago; he has never ceased to have sensations as if in the fingers. He imagines that he feels the hand in a bent position. He feels a pricking in the fingers, particularly when he lies upon the stump, so as to press the brachial nerves. I applied pressure to the nerves in the stump; and M. Schmidts immediately felt the whole arm, even the fingers, as if asleep.

e. My "commissionaire," during my stay in Leyden, had lost his arm by amputation above the elbow, twelve years before; but he had occasionally the sensation of tingling, as if in the fingers, particularly when he lay upon his arm.

f. Vir quidam in nosocomio Judaico Berolinensi, cui pes sinister, et alter cui brachium sinistrum amputatum erat, dicebant ambo, alter post hebd. 14, alter 17, se per operationem nihil commodi nactos esse; alter querebatur de dolore vehementi pedis, et alter brachii, cùm tamen non tam malè eos habuisset quam in primis hebdomadibus post factam operationem, et uterque non per hebdomades, sed per menses hosce, sensûs hujus fallacis diminutionem habere fatebatur. (Lemos, Dissert. inaug. quæ dolorem membri amputati remanentem explicat. Hal. 1798, p. 33.)

g. Nunc temporis etiam ibi versatur juvenis cui ante novem menses brachium sinistrum demtum est. In hoc eadem sensatio sub quinto et sexto mense post operationem decessit, sed mense octavo aliquot dies, ubi vehementior esse cœpit, habuit, ut interdiu

I do not speak of the dreams of individuals who have lost limbs by amputation, nor of the vivid perceptions such persons have of sensations, apparently in the entire limb which is lost, when the stump is pressed upon from the position of the body; for these are necessary consequences of the persistence of the internal sensations of the limb generally throughout life.

[Professor Valentin has observed, that individuals who are the subjects of congenital imperfection, or absence of the extremities, have nevertheless the internal sensations of such limbs being perfect. A girl, aged 19 years, in whom the metacarpal bones of the left hand were very short, and all the bones of the phalanges absent,—a row of imperfectly organised wart-like projections representing the fingers,—assured M. Valentin that she had constantly the internal sensation of a palm of the hand and five fingers on the left side as perfect as on the right. When a ligature was placed around the stump, she had the sensation of "formication" in the hand and fingers; and pressure on the ulnar nerve gave rise to the ordinary feeling of the third, fourth, and fifth fingers being asleep, although these fingers did not exist. The examination of three other individuals gave the same results.* These observations would seem to show, that in such imperfectly developed limbs the primitive nervous fibres destined for the absent parts are present. And if the cases examined by Prof. Valentin were not examples of spontaneous amputation during the fœtal state,† they would prove that arrest of developement does not always depend on deficiency of the nerves of the part.]

IX. *The relative position of the primitive fibres of the nerves at their origins and in the nervous trunks, is not altered by a change of the relative position of their peripheral extremities; and hence we find that, when the relation of the fibres at their peripheral extremity is changed, the sensations of which they are the seat are referred to the same spots as before.*— This is exemplified in the phenomena observed when the peripheral

tantum ope oculi et nocte ope manûs alterius jacturæ hujus se convincere possit. (Ibid. p. 33.) The author of the dissertation from which these cases are extracted, attributes the phenomena to the association between the two extremities, which is not a satisfactory explanation, for this association should first be explained.

h. A toll-keeper in the neighbourhood of Halle, whose right arm had been shattered by a cannon-ball in battle, above the elbow, twenty years ago, and afterwards amputated, has still (in 1833), at changes of the weather, distinct rheumatic pains, which seem to him to exist in the whole arm; and though removed so long ago the lost part is at those times felt as if sensible to draughts of air. This man also completely confirmed our statement, that the sense of the integrity of the limb is never lost.

i. A man whose hand had been amputated, had still, seven years afterwards, namely, at the time of his death, pains which seemed to him to have their seat in the hand. (Klein, in Graefe u. Walther's Journ. f. Chirurg. iii. 408.)

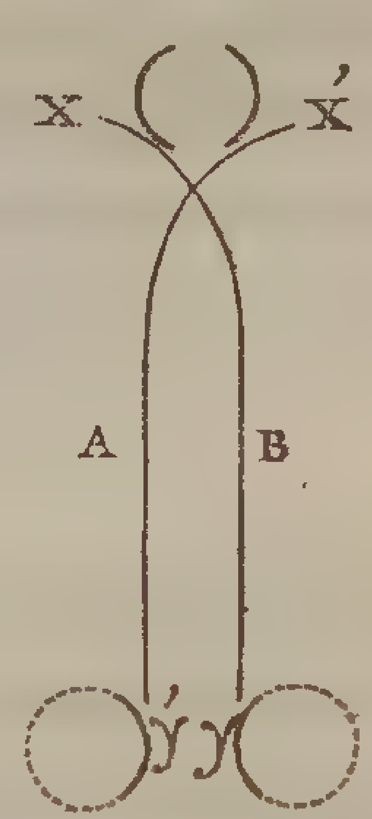
* Valentin's Repertorium für Anat. u. Physiol. Bd. i. p. 330.

† Such as are described in the papers of Dr. Montgomery in the Dublin Journal, vols. i. and ii. and of Dr. Simpson, in the 10th volume of the same journal.

extremities of nerves have their relative position changed artificially, as in the transposition of portions of skin. When, in the restoration of a nose, a flap of skin is turned down from the forehead and made to unite with the stump of the nose, the new nose thus formed has, as long as the isthmus of skin by which it maintains its original connections remains undivided, the same sensations as if it were still on the forehead; in other words, when the nose is touched the patient feels the impression in the forehead. This is a fact well known to surgeons, and first observed by Lisfranc. When the communication of the nervous fibres of the new nose with those of the forehead is cut off by division of the isthmus of skin, the sensations are of course no longer referred to the forehead; the nose is at first devoid of sensibility, but this is gradually developed in it.

Another phenomenon, perfectly similar in its nature to the foregoing, and explicable on the same principles, is that, when we cross the fore and middle fingers, and roll a small globular body—for example, a pea—between the opposed surfaces of the fingers, these surfaces being those which in the natural state are turned from each other, we seem to feel two globular bodies. When we touch a small spherical body with two fingers in their natural position, we do not in fact feel a globe, but merely two convex surfaces, which we imagine, or infer, to belong to a globular body. If, now, we cross the fingers, and make the two sides, which were previously external and turned from each other, internal and opposed to each other, the sensations, like the fibres in their connection with the brain, maintain the same relative position as if the fingers had not been crossed. In other words, the sensation produced by a convex segment of a sphere at X (see fig. 46) is felt at the opposite side at Y; and in the same way the sensation of X′ at Y′. The actual sensations produced at X and Y undergo no change; but, in consequence of their transposition, the impressions on the sensorium are those of two convexities (Y and Y′) turned towards, not from each other; and these the imagination converts into two complete spheres, since two convexities opposed to each other cannot belong to one sphere, but may to two.*

Fig. 46.



b. Of the radiation of sensations.

Occasionally it happens that one sensation excites another, or that sensations in disease extend to parts not actually affected. These phenomena are not rare in the state of health. Thus, the tickling sensation in the nose, excited by the influence of a strong light on

* This explanation of the above phenomenon, as well as the first principles of the laws of nervous action, was given in my Physiologie des Gesichtsinnes, Leipz. 1826, p. 84. The experiment was known to Aristotle.

the eyes, the extensive sensations arising from the excitement of a limited spot by tickling, the general sensations consequent on the irritation of the organs of generation in coitus, are of this nature; as also those excited by the near and startling report of a gun, and the sensations of trickling of water over the surface, and of shuddering, caused by hearing certain sounds, such as the scratching of glass, or by biting sandy substances. The pathological phenomena of this kind are, however, much more numerous: for example, the toothache extends from the situation of the irritating cause over the whole face; pain in one finger extends to the hand, arm, and the other fingers, without our being able in all cases to suppose that the morbific cause has been communicated to all these parts. The radiated sensations are more especially extended when excited by a tumour of a nerve, as in a case related in the Medical Gazette, 1834.* After amputation of the thigh, a swelling formed in the ischiadic nerve at its extremity, where it was also firmly united to the cicatrix and bone; here the skin of the entire stump, and sometimes even distant parts, such as the integuments of the abdomen, became affected with severe pain without any inflammatory symptoms; the stump being amputated at a higher point, the pains did not return. It is only necessary to hold for a certain time to a point of the skin a body of a burning temperature, to convince one's self that sensations can be produced in surrounding nervous fibres, which are not themselves immediately affected by the exciting cause. In the healthy state, such sympathetic sensations would be very inconvenient; hence nature has avoided their occurrence, by making the individual nervous fibres insulated in their action; for if the fibres from ten different points of the skin united to form one fibre before reaching the brain, but one impression from these ten points could be perceived by the sensorium, and it could be referred but to one spot; and if each primitive fibre in its course became actually united with nine other fibres which were continued isolated to the brain, the irritation of a single spot of the skin, even in the state of health, would be attended in its propagation to the brain by nine other sensations in other parts. Now, in the healthy state this does not usually occur; and it cannot, because of the isolation of the nervous fibres in their course to the brain. But there are cases which are exceptions to this rule; and how can the secondary sensations in such instances be accounted for? Since an impression at any point of the skin, if of sufficient intensity, will produce radiated sensations, the phenomenon cannot be attributed to anastomoses of the primitive fibres existing in some situations contrary to the general law. The explanation, whatever it be, must be applicable

* [Observations on the Neuralgic Affections of stumps after amputation, by Mr. J. F. Crookes. The rationale of the phenomena suggested by Mr. Crookes is very similar to the second explanation mentioned by Prof. Müller.]

to all the primitive fibres. Thus, reticulated anastomoses of the primitive fibres at their peripheral extremities is not adequate to account for the phenomena; for the radiation of sensations occurs in the retina, where certainly no such anastomosis of the fibres exists. Either of two hypotheses may be adopted.

The first presupposes the existence of certain properties in the ganglia of the sensitive nerves. Reil* compared the ganglia of the sympathetic nerve to imperfect conductors, and imagined that they do not communicate to the brain feeble impressions, but that, just as imperfect conductors of electricity permit the passage of large quantities of accumulated electric fluid, they are able to propagate very strong impressions, and also permit a limited influence of the brain and spinal cord upon the sympathetic nerve. Reil's hypothesis might be applied to the ganglia of the sensitive nerves: it might be said that this grey mass, through which the primitive fibres pass devoid of neurilema, is an imperfect conductor of the nervous influence, and therefore does not allow a feeble impression on particular fibres to be propagated through it to the other fibres, and hence that such impressions are transmitted merely along the primitive fibres on which they were originally made; but that, when the impressions are very energetic, the grey matter ceases to insulate the nervous fluid, and conducts off a part of it to the other primitive fibres which pass through the ganglion, thus giving rise to the radiated or sympathetic sensations.

According to the second explanation of these phenomena, the sympathetic sensations are the result of the radiation of the irritation from the fibres primarily affected upon the roots of other fibres in the brain or spinal cord; just as, in the production of the reflected motions, the impression conveyed by the sensitive nerves to the spinal marrow is communicated to motor nerves; the only difference being, that, when the sympathetic sensations are produced, the radiation of the impression does not reach the motor nerves, but only the sensitive fibres arising from the surrounding part of the cord, or at any rate affects these at the same time with the motor nerves.

The analogous case of the extension of irritation in the spinal marrow from the roots of the sensitive to those of the motor nerves, and the circumstance that sensitive nerves which have no ganglia, as the optic nerves, exhibit the phenomena of the radiation of sensations, are in favour of the latter hypothesis.

In what light now are we to regard the action of the sensitive fibres or sensitive nerves thus secondarily affected? Is it reflex action derived from the brain and spinal cord? Does a current pass from the cerebral or spinal extremity of the nerve in a retrograde course to its peripheral extremity; or if there is no current, but merely oscillation of a nervous principle, does the impression conveyed to the brain by the nerve pri-

* Archiv. für Physiol. Bd. vii.

marily excited, give rise to a reflex oscillation in another nerve from its cerebral to its peripheral extremity? It is exceedingly probable that there is, at all events, a reflection of the irritation from the spinal marrow or brain upon the nerve of sensation. It must be remarked, however, that if we explain the sympathetic sensations by such reflex action, we must presuppose that currents or oscillations can be propagated in the sensitive nerves in both directions,—from the brain as well as towards it. It is not known whether this be possible, or whether the sensitive nerves can propagate their actions in the centripetal direction only. It is interesting, therefore, to know that we can explain the phenomena, even though the sensitive nerves do not act in the centrifugal direction. We have seen (page 690) that the same sensation seems to be produced at whatever point of its length a nervous fibre is irritated, whether at its peripheral extremity, at its middle, or at its origin in the brain and spinal cord; and that this sensation is felt in the parts to which the nerve is ultimately distributed: the mere "radiation" of an impression, therefore, from one sensitive nerve in the substance of the brain or cord, so as to affect the origins of other sensitive fibres, will be sufficient to produce sympathetic sensations. We know in fact that, in affections of the spinal cord, the sensations appear to be in the peripheral parts of the body; thus inflammation of the spinal cord is attended with violent pain in the limbs. The radiation of sensations may have a similar cause.

c. Of the coincidence of several sensations.

Sensations appear to be clearly defined and distinct in proportion to the number of primitive fibres distributed to the part in which they are excited; the fewer the primitive fibres which an organ receives, the more likely is it that several impressions on different contiguous points will act but on one nervous fibre, and hence be confounded together, producing but one sensation. Prof. E. H. Weber* has made some interesting observations relative to the degree of distinctness of sensations in different parts of the body, as measured by the power of distinguishing distances. The experiments consisted in touching the skin with the arms of a pair of compasses the points of which were provided with pieces of cork, the eyes being closed at the time, and in ascertaining how close the two arms of the compasses might be brought to each other, and still each be felt distinctly. The experiments were numerous; the following are the results: the extremity of the third finger and the point of the tongue were found to be the parts of which the sensibility is most acute; a distance of as little as $\frac{1}{3}$ of a line being here distinguished. On the dorsum of the tongue the two arms of the compasses to be felt distinctly, that is, to excite two sensations, required to be separated to the extent of two lines. With the extremities of the fingers, and the point of the tongue, the distance could be distinguished most easily in

* Annotat. Anat. et Physiol. p. 44—81.

the longitudinal direction; on the dorsum of the tongue, on the face, the hairy scalp, the neck, and the whole arm, and the foot, the distance between the arms of the compasses could be recognised best when they were placed transversely. The following table shows the degree of sensibility of different parts as evidenced by the distances at which the two arms of the instrument could be felt as two distinct bodies.

Point of the tongue	½ a line.
Palmar surface of third finger	1 line.
Red surface of the lips	2 lines.
Palmar surface of second finger	2 ,,
Dorsal surface of third finger	3 ,,
Tip of the nose	3 ,,
The palm over the heads of the metacarpal bones	3 ,,
Dorsum of the tongue one inch from the tip	4 ,,
Part of the lips covered by the skin	4 ,,
Border of the tongue an inch from the tip	4 ,,
Metacarpal bone of the thumb	4 ,,
Extremity of the great toe	5 ,,
Dorsal surface of the second finger	5 ,,
Palm of the hand	5 ,,
Skin of the cheek	5 ,,
External surface of the eyelids	5 ,,
Mucous membrane of the hard palate	6 ,,
Skin over the anterior part of the zygoma	7 ,,
Plantar surface of the metatarsal bone of the great toe	7 ,,
Dorsal surface of the first finger	7 ,,
On the dorsum of the hand over the heads of the metacarpal bones	8 ,,
Mucous membrane of the gums	9 ,,
Skin over the posterior part of the zygoma	10 ,,
Lower part of the forehead	10 ,,
Lower part of the occiput	12 ,,
Back of the hand	14 ,,
Neck, under the lower jaw	15 ,,
Vertex	15 ,,
Skin over the patella	16 ,,
——— sacrum	18 ,,
——— acromion	18 ,,
The leg near the knee and foot	18 ,,
Dorsum of the foot near the toes	18 ,,
Over the sternum	20 ,,
The skin over the five upper vertebræ	24 ,,
——— over the spine near the occiput	24 ,,
——— in the lumbar region	24 ,,
——— in the middle of the neck	30 ,,
——— in the middle of the back	30 ,,
The middle of the arm	30 ,,
——— thigh	30 ,,

The distance between the arms of the compasses seemed to be greater when felt by the more sensitive parts than when it was estimated by parts of less distinct sensibility. When the points of the instrument were applied in a line drawn round the thorax, two spots

were found, namely, in the middle line before and behind, at which the sensibility was more defined than elsewhere. If the arms of the compasses were applied in the same line, but in the direction parallel with the axis of the body, four points were found especially sensitive; two of these were situated before and behind, in the middle line, and two at the sides. If the arms of the instrument were placed either transversely or longitudinally in a line drawn from the chin to the pubes, the sensibility was found to be most distinct on the chin, less so on the neck, again more distinct over the sternum, less so at the upper part of the abdomen, again more distinct at the navel, and indistinct in the neighbourhood of the os pubis. In the middle of the back the most defined sensibility was just below the occiput and over the coccyx. Along the side of the trunk, the most distinct sensibility was found in the axilla and in the groins.

The accuracy with which impressions are perceived does not depend essentially on the presence and number of the papillæ; for the sensibility of the nipple is indistinct, and the most acute sensibility of the tongue is limited to the tip: hence Weber supposes the difference of sensibility to depend on the number, course, and mode of termination of the nervous fibres. I coincide entirely in this opinion, and will merely remark, that the greater or less facility for the radiation of impressions in different parts of the brain and spinal marrow may have some share in the production of these differences.

The greatest power of distinguishing distances by sensation is possessed by the retina. It is interesting, with reference to the laws of sensations, to know that the size of the globules of the retina corresponds to that of the smallest sensible points on it. Weber found that the globules of the retina measure from $\frac{1}{8000}$ to $\frac{1}{8400}$ of an inch in diameter; the smallest angle of vision at which two points can be distinguished is 40″; hence Smith calculates that the most minute sensitive point of the retina measures $\frac{1}{8000}$ of an inch. Weber remarks, that when two impressions fall upon such a point, they will give rise to but one sensation.* Baumgaertner† attributes our indistinct perception of objects, of which the extent appears at a less angle than 13 seconds, to the physiological radiation.

A very remarkable instance of the coincidence or "identification" of sensations is afforded by two corresponding nerves of the opposite side of the body, namely, the optic nerves; no parallel case can be found in the whole body, and it must here depend on some special provision of structure. Impressions on the corresponding sensitive nerves of the right and left side in no other instance give rise to a single sensation. Similar impressions on the two hands are felt distinctly, not as

* Weber's edition of Hildebrandt's Anat. i. p. 165.

† Zeitschrift für Physik und verwandte Wissensch. ii, Bd. 3 Hft. p. 236.

one sensation; on the contrary, the two being conveyed to the sensorium give rise in it to two distinct sensations.

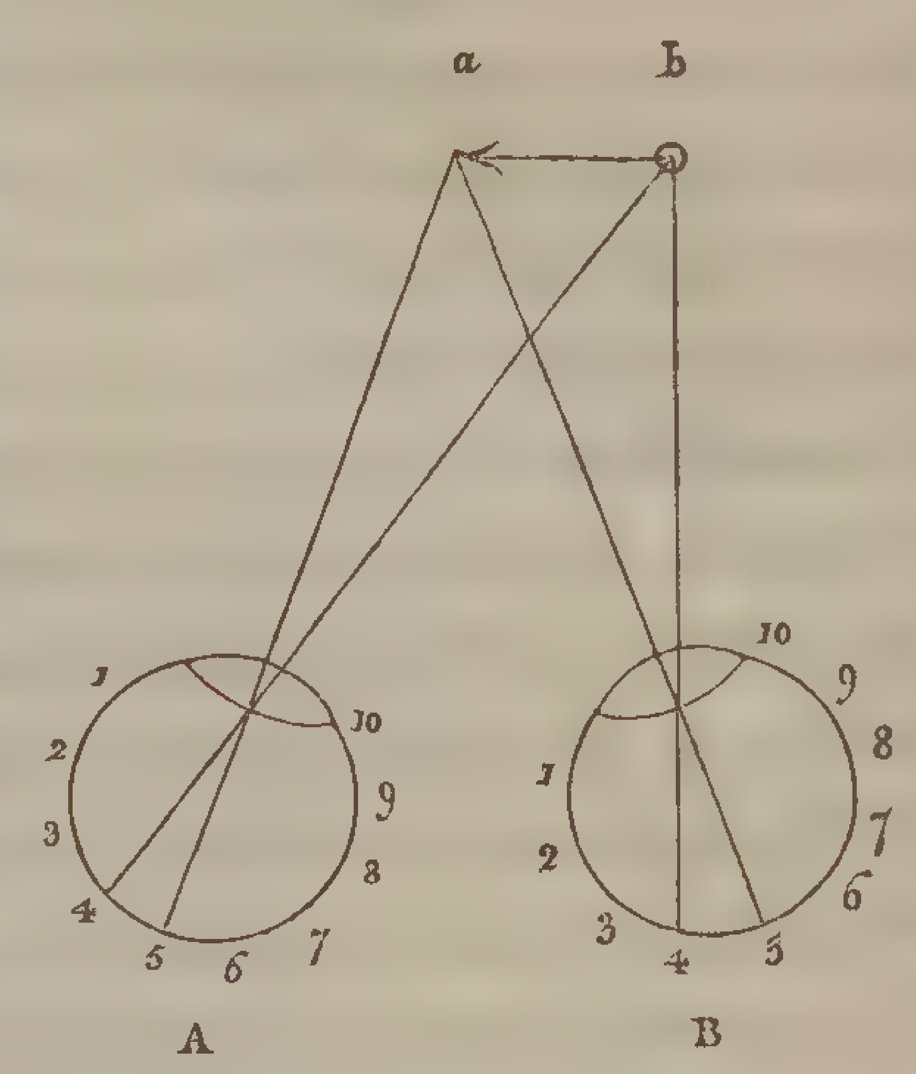
In the eyes or optic nerves, however, we meet with the anomaly that certain fibres of the one nerve with certain fibres of the other have but one and the same sensation, hence the phenomenon of single vision with two eyes. Some physiologists have maintained that we see with the two eyes alternately. But they who doubt that both are employed simultaneously can never have observed the frequent occurrence of double images of objects in the field of vision; one image belonging to one, the other to the other eye. Any one can convince himself of the fact by observing what occurs when we look at two objects placed at a little distance one behind the other; for example, two pins or two fingers. If the eyes be fixed upon the nearest finger, the axes of both being directed to it, the other finger will be seen double; if the eyes be directed to the furthest finger, the nearest is seen double; and by closing one eye, it will be readily perceived that one image of the object thus seen double belongs to the right eye, the other to the left.

The fact of there being certain parts of the retina or optic nerve of the two eyes of which the sensations are identical, and others of which the sensations are not so, may be proved by an experiment resting on the evidence of our own internal sensations—what is called a "subjective" experiment.

If we exert pressure on certain points of the globe of the eye, the eyelids being closed and light excluded, luminous spectra are produced by the pressure on the retina, and are always seen at the points opposite to those at which the pressure is made. If the eye be pressed below, the image appears above; if the pressure be applied above, it is seen at the lower part of the field of vision; if on the right side, the image is on the left; and *vice versâ*. If now the left side of both eyes be pressed upon, there will be, in place of two images, but one produced; if, on the contrary, pressure be made in one eye on the right side, and in the other on the left, two figures are seen at the opposite sides of the field of vision. If both eyes be subjected to pressure at the upper part, one image is seen below; if the pressure be applied in both below, a single image is formed above. But if one be pressed upon below, and the other above, two images will appear; one above, the other below. In performing this experiment, the pressure must not be made at the anterior part of the eyes, because no retina lies there; the pressure must be applied deeply. These experiments alone are sufficient to prove the identity of the sensations at certain points of the retina of the two eyes, and the difference of the sensations at other points: in reference to sensations, the two retinæ must be regarded as included one within the other; so that all points of the two retinæ which lie within the same degrees of latitude and longitude (the eyes being regarded as globes) are identical

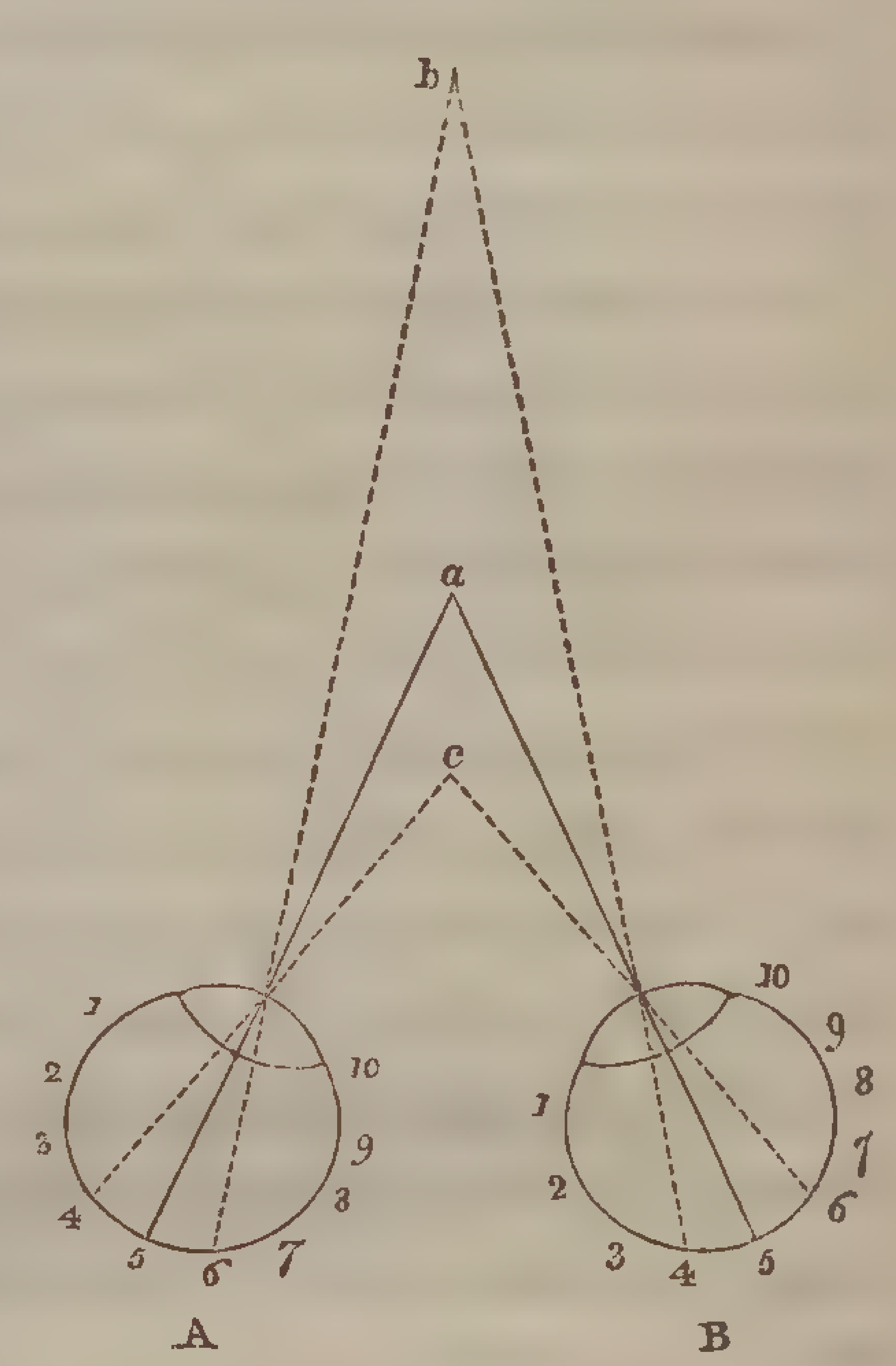
in their sensations; all other points in the two retinæ are opposed to each other, or different, just as any two points in the retina of the same eye. This may be proved still more distinctly in a different manner.

Fig. 47.



In the figure (fig. 47), the axes of both eyes are directed to the point *a*; the retina being divided into ten equal parts, the point *a* will in each eye fall at 5; the point *b* will in each eye appear at an equal distance to the left of 5, namely, at 4. Thus the image occupying in both eyes the space between 4 and 5 will be seen single, for these spots are identical; the points marked with the corresponding numbers in the two eyes are identical. If the image does not fall on such identical points, it will appear double, thus:

Fig. 48.



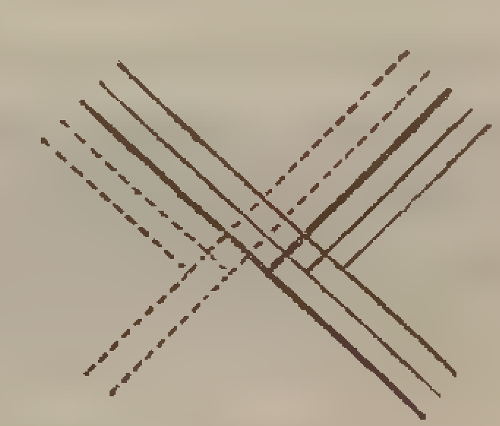
In figure 48, the two eyes are fixed upon the point *a*, their axes are directed to it: if this were an object, it would appear single, while every thing behind or in front would be seen double. The point *b*, for example, throws its image in the eye A at 6, in the eye B at 4, points of the retina which are not identical. The object *b* is seen double; and the distance between its two images is, in comparison with the whole field of vision, in the proportion of the space from 6 to 4 to the space occupied by the compartments 1 to 10, and their position would be as 6 and 4. The point *c*, on the contrary, throws its image in the eye A at 4, in the eye B at 6; it is likewise seen double. Hence it is that when two fingers are held one before the other, and the eyes fixed upon one, the other is seen double.

It is evident, therefore, that the two globes of the eyes are most minutely divided into degrees, minutes, and seconds of latitude and longitude; that at all corresponding points they are identical, at all different points non-identical; and that in double vision the distance between the two images may always be determined by the distance found to exist between the two points on which the impression is made in the two retinæ, supposing these to lie one upon the other.

Since the optic nerves differ from all other nerves in conveying to the

sensorium the sensation of but one impression, when certain points of the two retinæ are simultaneously affected, and since all other nerves agree in their primitive fibres being distinct in their whole course, the supposition naturally arose that the optic nerves differ in the organisation of their primitive fibres,—that the fibres of the two nerves are connected with the brain at one point only instead of two. This cannot be proved, it is true, with reference to the individual primitive fibres generally; but it is demonstrable with regard to their fasciculi. For, as is well known, each root of the optic nerves, on leaving the commissure or chiasma, does not go to one eye solely, but to both eyes; the external fibres of each root being continued at the side of the commissure to the outer side of the corresponding optic nerve, while the internal fibres cross to the inner side of the nerve of the opposite side; so that the external portion of the retina of one eye, and the internal portion of that of the other, are formed by one root of the optic nerve, or, in other words, the left portions of the two retinæ are formed by the two branches of the left root, the right portions of the retinæ by the two branches of the right root of the optic nerves, which entirely corresponds with the phenomena of single vision. This theory of single vision was proposed by Newton, and has since been again put forward by Wollaston. But the mere division of each root of the optic nerve into two branches to form the identical corresponding parts of the two retinæ, does not completely account for the phenomena; for the left half of the retina A, from 1 to 5, (fig. 47,) is not as a whole identical with the left half of the retinæ B from 1 to 5, but certain points only of the left half of both retinæ are identical, namely, those which in the two retinæ occupy the same degrees of latitude and longitude; 1 is identical with 1, 2 with 2, and so on; but 1 in the one eye is not identical with 5 in the other eye. Hence, to explain the single vision, it is necessary that not merely each root of the optic nerve, but each primitive fibre of each root, should in the chiasma divide into two branches for the two optic nerves; so that the identical fibres of the two nerves might communicate with the brain at one point only, namely, by one radical fibre, and hence, though receiving two impressions, they might communicate but one to the sensorium. (See fig. 49.) But such a division of the fibres in the chiasma does not exist, and several facts are opposed to the supposition of its existence. In the first place, were such the case, each optic nerve between the commissure and retina ought to be twice as thick as each root of the optic nerve between the brain and commissure; and, secondly, every point of the retina ought to be the end of a fibre of the optic nerve. Were this the case, all the fibres which rise to the inner surface of the retina towards its anterior part, ought to be aggre-

Fig. 49.



gated together at its posterior part, so that the retina would diminish in thickness from behind forwards. Again, in an injury on one side of the brain, the corresponding half of each retina ought to be paralysed; whereas, in such a case, either the one or the other eye is blinded entirely, and in animals it is always the eye of the opposite side which is affected.

CHAPTER III.

OF THE REFLECTION IN THE PRODUCTION OF MOTIONS CONSEQUENT ON IMPRESSIONS UPON SENSITIVE NERVES.

The occurrence of motions consequent on sensitive impressions has been known, not merely to the earlier physiologists, but to the cultivators of medicine in all ages. Physiologists have generally followed Willis in ascribing them to nervous communication by means of the ganglionic or sympathetic nerve, which hence acquired the latter epithet. Comparetti* wrote an entire work for the purpose of explaining the morbid consensual phenomena by communications between nerves. These views were adopted by most physiologists; and even very recently† new anatomical facts relating to the nerves have received applications agreeing with them.‡

* Occursus Medici. Venetiis, 1780.

† See Tiedemann, Zeitschrift für Physiol. i. 1825.

‡ [The sympathetic movements seem to have been generally attributed by physiologists in Germany, during the last few years, to nervous communications; such, however, has not been the case in this country. The opposite view has been adopted by all English authors who have published original works on physiology. Dr. Alison (Outlines of Physiology, 1831, and Transact. of the Med. Chir. Society of Edinb. vol. ii.) adopts the opinions of Whytt and Monro; the sympathetic motions, such as the ordinary movements of respiration excited by changes in the lungs, those of sneezing and coughing by irritation of the nostrils or trachea, the movement of vomiting by irritation in the stomach, &c. are ascribed by Dr. Alison to the influence of peculiar sensations transmitted to the brain; it being impossible, he contended, to explain them on the anatomical principles of connections among the nerves of the sympathising parts. Dr. Bostock (Elements of Physiology, 1827, vol iii. p. 224.) is equally decided in denying the agency of the sympathetic nerve in conveying the influence which excites the sympathetic actions; and with respect to the necessity for the intervention of the brain in the production of the movements, he says, speaking of Whytt's arguments on the subject, "The facts which he adduces are of such a nature as, I think, to prove that the co-operation of the brain is essential in those actions which we refer to the operation of sympathy." Mr. Mayo, (Outlines of Physiol. 2nd Edit. 1829,) does not treat separately of the sympathetic movements; but it is evident from his explanation of one of them,—the contraction of the iris under the influence of light,—from his remarks upon the associated origins of the cerebral nerves, (p. 343,) and from his observations on the sympathetic nerve, (p. 339,) that he regarded them as taking place by the intervention of the central organs of the nervous system, and not through the medium of anastomoses of the nerves.]

Some even of the earlier physiologists, however, as Haller, Cullen,* Whytt,† Monro,‡ and others, were dissatisfied with this theory of sympathies. Whytt and Cullen believed the phenomena to take place through the intervention of the sensorium, and to be consequent on sensations. It is but very recently, however, that these sympathetic motions have been investigated in an exact and experimental manner. Several important facts, unfavourable to the hypothesis of these phenomena, being dependent on the sympathetic nerve, were noticed by Mayo § in 1823. It had been usual to attempt to account for the fact of the motions of the iris being determined by the influence of light on the retina by communications supposed to exist between the optic nerve and the sympathetic. In Mr. Mayo's experiments, however, on the nerves of the eye with reference to the motions of the iris, it was shown that these motions are effected by the action of the third nerve, and excited by irritation of the optic nerve (as by stretching it), hence proving that the phenomenon must be produced through the medium of the brain. After dividing the optic nerve within the cranial cavity in a pigeon, he was still able to excite contraction of the pupil by exerting traction on the portion of the optic nerve still connected with the brain. The principle of the reflection of the irritation from the sensitive upon the motor nerves through the medium of the central organs of the nervous system, was, however, first shown to be generally applicable in the explanation of all motions consequent on sensations, by the researches of Dr. Marshall Hall|| and myself, published in 1833, in which the theory was established by new facts to be the true mode of explaining a great number of known but ill-understood phenomena.¶

* Institutes of Medicine, pt. i.

† On Sympathy and Nervous diseases (in the German edition of Whytt's works, p. 241.)—An Essay on the Vital and other involuntary motions. Edinb. 1751, p. 248.

‡ On the Nervous System. (Leipzic edition, 1787.)

§ Anatom. and Physiol. Commentaries.

|| The paper of Dr. Hall, which is here referred to, appeared in the second part of the Philos. Transactions for 1833. I first stated my views in the first edition of the first part of this work, which appeared in the spring of that year, in the chapter on the respiratory movements, and more fully in the second part of the work in the following year, 1834, after Dr. Hall's paper had appeared. A paper by Dr. Hall had, however, been read at the Zoological Society on this subject in 1832; he has, therefore, the priority. Dr. Hall published an account of my views, and a comparison of them with his own, in the Lond. and Edinb. Mag. vol. x. no. 58.

¶ [Here Professor Müller is certainly in error. Earlier physiologists have taken an extended view of the sympathetic or reflected motions; they have recognised the principle of their dependence on an impression conveyed to the brain and spinal cord, have distinguished them from the motion dependent on consciousness and volition, and have even indicated the parts of the central organs of the nervous system which are capable of reflecting impressions communicated to them by sensitive nerves, so as to excite motions. Glisson (Tract. de Ventriculo, 1677, p. 172,) speaks of an influence

A later work* by Dr. Hall contains the continuation of his researches. The facts observed by Dr. Hall and myself are very similar, but we differ much in our mode of explaining them. I have brought forward arguments in favour of the old opinion of the concurrence of the central organs in the sensations and motions. Dr. Marshall Hall, on the contrary, in his last work, introduces an entirely new principle into the explanation, which is thereby rendered quite distinct from that which I adopt. Volkmann† has added several important facts confirmatory of the doctrine of reflex action. The following is my view of the subject, as given in the former edition of this work, together with a sketch of

being "reflected" from one nerve, at its origin, upon other nerves, so as to cause consensual movements. But it is to Dr. Whytt, who, with Dr. Monro, contended against the doctrine of sympathy by nervous communications, that we owe the first and most comprehensive generalisation of the sympathetic movements of health and disease, with which he associated those excited by mechanical irritation in animals, even after decapitation, as long as the spinal cord remains entire. — (Whytt's works, p. 506.) He supposed the brain and spinal cord to have the power of regulating the phenomena in question by virtue of the "mind or sentient principle" seated in them, which in causing the voluntary motions acts as a rational agent, but which, under the influence of peculiar sensations transmitted to it, acts "necessarily, and without previous ratiocination, for the preservation of the body."—(P. 153, 162, and 511.) Dr. Whytt's theory of the sympathetic movements was adopted with some modifications by Haller and Cullen. Dr. Cullen, however, rejecting the Stahlian doctrine of a "sentient principle" or "soul," was enabled to distinguish more definitely these actions excited by internal or external impressions communicated to the brain, from the effects of sensation and volition.—(Works, vol. i. p. 109, et seq.) Unzer had already, in 1771, approached still nearer to the present theory of reflex nervous actions. Thus, in his "Erste Grunde einer Physiologie," p. 349, he says, "The external sensitive impression on the nerves, therefore, even although it does not reach the brain, and consequently is not perceived or felt, may nevertheless give rise to the same animal motions in the body as if it had been perceived;" but he seems to refer the reflection of the impression not to the central organs, but to the ganglia. The views of Prochaska, however, were more definite, at the same time that they were more general. He attributed the numerous phenomena previously known to one particular mode of action of the nervous system,—"the reflection of sensorial impressions upon motor nerves;" and he traced the limits of the parts of the nervous system in which this reflection can take place. He regarded the cerebrum and cerebellum as the seat of the mind, or as the instrument by which it acts; while in the medulla oblongata, crura cerebri cerebellique, part of the optic thalami, and all the spinal marrow, "in a word," he says, "in all the parts from which nerves arise," he placed the "sensorium commune," or the seat of the reflection of sensorial impressions on motor nerves. As one law governing the reflex actions, Prochaska pointed out the law of self-preservation (nostri conservatio). He taught, moreover, that the reflected motions may take place either with or without the cognizance of the mind. All these points he illustrated by numerous examples derived from the natural actions of the body, the phenomena of diseases, as the different kinds of convulsions, and experiments on decapitated animals. The movements of the fœtus in utero were likewise classed by Prochaska among the reflected movements. These views were published by Prochaska in his Annotat.

* Memoirs on the Nerv. Syst. Lond. 1837.

† Müller's Archiv. 1838. Heft. i.

Dr. Hall's investigations, and a comparison of the different views offered to explain the phenomena.

When impressions made by the action of external stimuli on sensitive nerves give rise to motions in other parts, these are never the result of the direct reaction of the sensitive and motor fibres of the nerves on each other; the irritation is conveyed by the sensitive fibres to the brain and spinal cord, and is by these communicated to the motor fibres.—This law, which is of extreme importance in physiology and pathology, from its explaining

Academicæ, in 1784; and in 1800, in his Opera Minora (pt. ii. p. 150, et seq.); and were restated by him in his Institutiones Physiologiæ, 1808, t. i. p. 99. The researches of later physiologists merely afford confirmation of the theory thus completely laid down by Prochaska. The motions which continue in decapitated animals, particularly under the influence of irritation applied to the surface, were known to many of the older physiologists. Sir G. Blane connected with them the phenomena of instinctive actions, such as the act of sucking on the contact of the nipple, and the act of the first inspiration on the first contact of the air; and drew the inference that such instinctive or automatic movements, being independent of the brain, are not dependent on sensation.—(Select Dissertations, p. 261.) Legallois, from similar experiments to those of Sir G. Blane, came to a different conclusion, namely, that sensation and volition may continue independently of the brain; he did not, therefore, distinguish the movements which continue in the body after decapitation, from voluntary movements. He showed, however, clearly, by experiment, that one group of natural reflected movements—the respiratory—are dependent on a particular part of the spinal cord; and, by dividing the spinal cord at different points, and destroying different regions of it, he demonstrated that the movements excited by pinching different parts of the body of a decapitated animal are dependent on that part of the spinal cord from which the part irritated receives its nerves.—(Legallois, sur le principe de la Vie, 1812, pp. 32—34 and 60.) Similar experiments were performed afterwards by Mr. Mayo and M. Flourens. When Mr. Mayo published his experiments, the discovery of the sensitive and motor roots of the spinal nerves had been made; hence he was enabled to express in new terms the fact of the transmission of an influence "from the sentient nerve of a part to the corresponding motor nerve, through the intervention of that part of the nervous centre to which they are mutually attached."—(Anat. and Physiol. Comment. 1822, pt. ii. p. 135.) He distinguishes the motions thus excited from the consequences of volition, but not from those of sensation. Flourens distinguishes the influence on which these actions depend, both from sensation and volition; he attributes the phenomena in question to the property of "excitability" (the power of exciting motions in muscles), which he refers to nearly the same parts of the nervous centres as had been pointed out by Prochaska to be the seat of the principle which he called the sensorium commune. Sensation and volition he places in the cerebral hemispheres.—(Sur le Système Nerveux, p. 22.) Flourens states, as one of his conclusions, that it is through the medium of the spinal cord that the generalisation of the irritation, or the general sympathies, are established (p. 15); but he does not explain his views on this point. The only natural movement which he distinctly mentions as being excited by an irritation conveyed to the central organs, is the contraction of the iris from the influence of light. Since the time of Prochaska, no physiologists had shown the general applicability of the principle of the reflex action of the nervous system, as distinguished from the results of sensation and volition, until it was done by Dr. Hall and Professor Müller.]

a great number of phenomena, requires to be strictly proved, and this can be done by experiment.

I will, in the first place, demonstrate that, after the union of the two roots of a nerve, the sensitive and motor fibres themselves do not unite, but are continued quite distinct from each other to the parts which they respectively supply; and that hence, in the cases also where nervous sympathy is not in play, the sensitive and motor fibres in the nerve itself have no reciprocal action on each other. This may be easily proved in the following manner: having divided a mixed (motor and sensitive) nerve, irritate the portion of it which is connected with the brain or spinal cord; violent pain will be produced, which the animal may express by movements of flight, by cries, &c.; but the motor fibres of the branches coming off from the irritated portion of the nerve are not excited to action, no contractions of the muscles to which they are distributed take place.

The same truth may be demonstrated by another method: the three nerves which supply the lower extremity in the frog form, as we have already mentioned, (page 68,) a plexus from which two nervous trunks issue; if now, one of these be divided, isolated from all its connections with muscles, and the portion of it connected with the plexus irritated, the impression will be transmitted in the centripetal direction by the sensitive fibres of the nerve, but the motor fibres of the other nerve arising from the plexus are not affected, and excite no contractions in the muscles to which they are distributed.* The general convulsions excited by merely touching a frog or other animal in a state of narcotisation may likewise be clearly shown to be owing to an influence of the spinal cord and brain themselves; for, if a limb of a frog in such a state be cut off, a touch no longer excites contractions of the muscles of the limb. The experiments on the land or spotted salamander are still more instructive.

This animal retains, for an extraordinary length of time after the spinal cord is cut through, the sensibility of all parts below the point of division, or, if the term sensibility be objected to, the power of propagating impressions to the spinal cord, and of reacting by contractions of the muscles. Even the extremity of the tail preserves its sensibility to impressions; the property is in fact heightened by division of the spinal cord, just as it is in frogs, by narcotisation. The slightest touch of a separated portion of the trunk of the salamander excites muscular con-

* [Since in this and the foregoing experiment the nerve irritated was not cut off from connection with the central organs, it appears at first sight that reflex motions ought to have been induced by the impression conveyed to them. The opposite result can only be explained on the consideration that the spinal cord was not, as in the succeeding experiments, thrown into a state of irritation by division or narcotisation, and that irritation of the trunks of nerves does not so readily excite the reflecting action of the spinal cord as impressions on their cutaneous extremities.]

tractions in it: this excitability is preserved for hours. But it is necessary that a portion of the spinal cord should be contained in the part of the body made the subject of the experiment; the phenomena are not produced in an entire limb if no portion of the spinal cord is connected with it. I observed these interesting facts several years ago (in 1830), when performing some experiments with M. Jordan on the poison of the cutaneous gland of the salamander.

It appears, then, that the general spasms excited in animals by touching points of the surface do not depend on a communication between the sensitive and motor fibres in the nerves, but that the spinal cord is the essential link between the centripetal impression conveyed by the sensitive fibres and the centrifugal influence of the motor nerves. The above facts prove likewise that the phenomena of general spasms thus excited are not dependent on the sympathetic nerve, but that they are owing to an irritation of the spinal cord, by virtue of which every impression conveyed to it by the sensitive fibres, even though quite local, is propagated through the whole spinal cord and brain, and thus necessarily excites all the motor fibres given off from them. The state of irritation of the spinal cord here referred to may, however, be produced by any of the following causes:—

1. In many animals, by the mere division and contusion of the spinal cord. Thus, every touch excites general spasms in the tortoise after its decapitation; the same phenomenon is produced in very young birds, if they are touched the very moment after they are decapitated, and, as we have shown, in all parts of the trunk of the land salamander after it has been cut into many segments.

2. The same degree of irritation of the spinal cord exists in frogs during the first stage of poisoning by narcotics; and also in mammalia, in which, after poisoning by nux vomica, general spasms are immediately produced, when they are laid hold of at any part or in any manner. This state of excitable exhaustion (reizbare Schwäche) almost always precedes the stage of paralytic exhaustion.

3. Other causes, also, which produce exhaustion of the brain and spinal marrow, by excessively exciting them, give rise to the same phenomenon. In persons in whom the nervous system is in that state of exhaustion which is accompanied with great excitability, every sudden impression on the nerves, whether by sound, touch, or mechanical shock, causes the whole frame to start. Such a state of the spinal cord is produced by excitement of the generative organs, and through them of the spinal cord, and by other causes. We may here remark, that any excitement of the nervous system may induce three states in succession. First, the state of excitement with the powers unimpaired; secondly, in proportion as the excitation is repeated, a state of exhaustion with excitability; thirdly, atonic exhaustion.

4. Severe local irritation of a sensitive nerve may, by the intensity of the impression conveyed to the brain and spinal marrow, give rise to twitchings of the muscles and tremours, as we observe to be produced by severe local burns, extraction of a tooth, &c.

5. Local irritation of the nerves, from inflammation or ganglionic enlargements, also frequently gives rise to general spasms, even to epilepsy.

6. The irritation of the spinal cord, arising from local excitement communicated by sensitive fibres, may be so intense that the spasms are constant, and continue without any new stimulus, such as the contact of a substance with the surface. Such is tetanus traumaticus, a violent irritation of the spinal cord, arising from severe injuries of the nerves. Every intense irritation of the spinal marrow generally is tetanus, whether it be caused by narcotic poisons acting directly upon it, or by local irritations conveyed to it through the nerves. The production of tetanus is intelligible, if the above facts established by experiment are taken into consideration.

7. Great irritation of the sympathetic nerves in the intestinal canal, likewise, by being propagated to the central organs of the nervous system, gives rise to secondary general cramps: it is thus that we must explain the cramps in sporadic cholera, and in intestinal affections in children.

From the facts thus far considered, we are led merely to admit as a law, that, whenever general spasms are excited by local impressions, the phenomenon depends on no other communication between the sensitive and motor fibres than exists in the spinal cord. In very many cases, however, local irritation of the nerves gives rise, not to general, but to local muscular spasms; in which case, again, the spinal cord is to be regarded as the bond of communication between the sensitive and motor fibres. The cases of this kind are the following :—

1. The most simple is that in which the local irritation of the sensitive fibres being propagated to the spinal cord or brain excites merely local spasms; in those parts, namely, the motor fibres of which arise from the spinal cord, near the point where the sensitive fibres that are irritated also take their rise. Of such a case we have instances in the spasms and tremours of limbs on which a severe burn is inflicted, &c. Certain parts of the frame which are exceedingly excitable,—for example, the iris,—are very readily made to contract, even when only feeble stimuli affect other sensitive nerves. It has been long known that the action of light on the iris itself does not excite its contraction, that the light affects the iris through the medium of the optic nerve and brain; for this was proved by the experiments of Lambert, Fontana, and Caldani. Rays of light, passed through a small cone of paper, or through a hole in a sheet of paper, and directed so as to fall through the pupil upon the retina, excite immediate contraction of the iris, but have no such influence when made to fall upon the iris itself.

The iris of an amaurotic eye, again, is fixed as long as the sound eye is closed, but contracts when the sound retina is exposed to the stimulus of light. The exceptions to this rule, in which the iris of amaurotic eyes has possessed mobility,* may have been cases of imperfect amaurosis; or, if only one eye was amaurotic, the motion of the iris in the diseased eye might have arisen from the other eye being open. The state of the iris in an amaurotic eye can and ought to be examined only with the sound eye closed. When this circumstance is not attended to, the observation cannot be conclusive. Van Deen,† after removing one hemisphere of the brain in a rabbit, and dividing the optic nerve on the same side, found, on exposing the eye to light, that the iris still contracted, and hence concluded that the optic nerve has no influence over the iris. But, inasmuch as he held the light before both eyes, (ante oculos,) the result is easily explained. It is possible, however, for the sensation not to be perceived by the brain, and the nerve, nevertheless, to be capable of the reflex action. Tiedemann's interesting discovery, that the arteria centralis retinæ is accompanied by a minute branch from the ciliary ganglion, will not explain the phenomenon of the contraction of the iris: for all vessels are accompanied by nerves; and this branch which accompanies the artery of the retina in its distribution, has not been shown to have any connection with the substance of the retina itself. The reflex motor action of the brain upon the iris is effected through the medium of the third nerve, irritation of which has been shown by Mr. Mayo to be always productive of contraction of the iris. Mr. Mayo has likewise shown, that, after dividing the optic nerve, we can, by irritating that portion of it which is connected with the brain, excite contraction of the iris. In the action of the iris there appears, then, to be a kind of balance (statik) of excitement established between centripetal sensitive and the centrifugal motor action through the medium of the brain. Other nerves besides the nervus opticus are capable of disturbing this balance; thus, cold water drawn into the nose, by stimulating the sensitive branches of the nervus trigeminus, causes the iris to contract. Among the simpler cases of reflected excitation, may be instanced also the winking of the eyelids under the long-continued influence of light, or in consequence of a loud noise, or of a threatening impression on vision.

In the case also of the contractions of all the perineal muscles in expelling the semen, which are excited by irritation of the sensitive nerves of the penis, the spinal cord is the medium of communication between the sensorial impressions and the movements. In muscles laid bare, the irritation applied directly to them acts also on the motor fibres distributed in them, and contractions of them are excited without any

* See Tiedemann's Zeitschrift, i. p. 252.

† De differentiâ et nexu inter nervos vitæ animalis et organicæ, p. 58.

centripetal and centrifugal action of the nerves. But muscles which are invested by sensitive membranes, and are not themselves exposed to direct stimulus, can only be excited to action by irritation of the sensitive property of their investing membrane, the transmission of this irritation to the brain, and the centrifugal propagation of the motor influence from the brain to themselves. Thus the contractions of the glottis and air-passages, excited by the contact of irrespirable gases, are not the immediate result of the irritation of the parts themselves, but of the excitement of the sensitive fibres and the reflected influence on the motor nerves. Brachet has demonstrated this more fully. When the vagus nerve has been divided on both sides, a chemical irritant introduced into the trachea of the animal does not excite coughing, which, when produced by irritation of the air-tubes, depends on centripetal and reflex action. [The movements of deglutition also belong to this class. The sensitive nerves which transmit the impression to the nervous centres, are, according to Dr. Reid,* the glosso-pharyngeal and superior laryngeal nerves and branches of the fifth upon the soft palate and isthmus of the fauces. The motor nerves for these movements are the pharyngeal branches of the par vagum. The contractions of the œsophagus also are, as shown in another place, owing to reflex nervous action. It would appear from Dr. Reid's experiments (see p. 657) that the sensitive and motor fibres of the pneumo-gastric afford the medium of transmission for the reflex influence.] The same explanation applies to the contractions of the sphincter ani and sphincter vesicæ. The muscles cannot be themselves stimulated by the excrement and the urine, but these matters act on the sensitive nerves of the mucous membrane and excite the spinal cord, which, as if constantly charged with motor influence, reacts upon the muscles; hence, after injury of the spinal marrow, these muscles cease to act.

2. The second case is, where the excitement of the sensitive nerves is entirely local, but the reflected influence from the brain more extended. Of this we have an instance in the phenomena accompanying coughing; in which not merely the vagi, but, to produce the contractions of the thoracic and abdominal muscles, the spinal nerves also are called into action. A number of spasmodic movements of the organs of respiration, as sneezing, hiccough, vomiting, &c. are produced in the same manner; they all arise from irritation of the pulmonic and intestinal tracts of mucous membrane, that is to say, from irritation of the sensitive nerves of these parts, which is propagated to the brain, and there excites to action the source of motor power for the respiratory movements in the medulla oblongata. [According to the later views of

* [See page 652, and Dr. Reid's paper on the Eighth Pair of Nerves in the Edin. Med. and Surg. Journ. No. 134.]

Dr. Hall, the medulla oblongata is not the essential primum mobile of the respiratory movements. The acts of respiration are, according to him, under ordinary circumstances, reflected actions excited through the medium of the pneumo-gastric nerves, and they continue as such even when the brain is removed. But when the nerves just mentioned are divided, respiration is continued as a voluntary act by the influence of the brain. If the brain is removed, and the pneumo-gastric nerves divided at the same time, respiration ceases. The respiratory movements can be excited also, as is well known, by the application of cold to the sensitive nerves of the surface.] We have already noticed in the section on respiration the remarkable circumstance, that the whole system of respiratory nerves can be excited to action by irritation of any part of the mucous membranes, from the mouth to the anus, from the nostrils to the lungs. The mode of production of sneezing we have already explained (page 353). It has been denied that sneezing is the result of irritation reflected from the brain upon the muscles engaged in its production; and in proof it has been stated, that a man who had lost the sense of smell could still be made to sneeze by means of snuff. There is certainly no reason why he should not; for, although the olfactory nerves were absent, the common sensitive nerves of the nose—the nasal branches of the fifth—would still be susceptible of a tickling sensation as in other persons. But, let us examine how the explanation of a sympathetic action by means of the sympathetic nerve will accord with anatomical facts. How can sneezing be explained by nervous communication? In the first place, there does not appear to be the most remote reason to explain why irritation of the sympathetic nerve in the nose should give rise to sneezing, rather than to many other movements, for example, an increased activity of the intestinal movements. Then, again, the explanation is not satisfactory; because, when the sympathetic nerve becomes connected with other nerves, its fibres do not actually unite with those of the other nerve. In sneezing, for instance, all the muscles of expiration are thrown into strong contractions, for the production of which all the fibres of the intercostal nerves must have suffered irritation. But how can the irritation be communicated to them by the sympathetic nerve? for, although each of the intercostal nerves communicates with it by a connecting branch, this branch, so far from conveying fibres from the sympathetic to unite with all the primitive fibres of the intercostal nerves, is rather the means of conveying fibres from the spinal cord to the sympathetic nerve? Now, since primitive nervous fibres are incapable of communicating any influence to other fibres which merely lie in contact with them, particularly in the motor non-ganglionic roots of nerves, the sympathetic affection of all the primitive fibres of an intercostal nerve by the influence of the nervus sympathicus, is quite an impossibility. All these sympathetic affections,

sneezing, coughing, vomiting, &c. are easily understood, now that we are acquainted with the reflex function of the spinal cord and brain, and know that all the respiratory nerves (the facial, vagus, spinal accessory, phrenic, and the other spinal respiratory nerves,) are, by reason of their origin from the medulla oblongata, or their subjection to its influence, prone to be excited to the production of convulsive movements in muscles, by any irritation communicated by the sensitive nerves of the mucous membranes to the spinal cord or medulla oblongata.

Any considerable irritation in the intestines or urinary organs has a tendency to produce contraction of the diaphragm and abdominal muscles, by which a diminution of the cavity of the abdomen is produced, and its contents expelled by the mouth when in the stomach, or otherwise by the anus, the urinary organs, or the generative organs, as in parturition. The expulsion of the fœtus in some cases after the death of the mother, and the fact that the finger introduced into the pharynx of a decapitated animal is tightly seized, show us the importance and intimate connection with life of this property which the spinal cord enjoys of issuing its motor influence when its sensitive nerves are affected with a local stimulus. If the sympathetic plays any part in the production of these phenomena, for instance, in vomiting, it consists merely in its conveying, like all other sensitive nerves, the impression made upon it to the sensorium. In fact, by irritating the splanchnic nerve with a needle, I have been able to produce contractions of the abdominal muscles in rabbits. (See page 508.)

3. In the second kind of cases, the reflex action affects a large group of nerves—the respiratory nerves, and it is excited most frequently by irritation of a mucous membrane; when the irritation is more intense, however, the effects may be still greater, affecting almost all the nerves of the trunk, if the irritation of the spinal cord becomes extensive. Thus, in severe cases of sporadic cholera (the Asiatic cholera I do not refer to, on account of the obscurity of its nature,) sometimes cramps affect even the trunk.

4. In the reflected motions produced by violent impressions on the sensitive nerves of the skin, not of the mucous membranes, the respiratory movements are not sympathetically excited, but rather spasmodic contractions of the muscles supplied by the whole system of nerves of the trunk, without any spasmodic movements of respiration. Of the extreme degree of such an affection we have instances in the epileptic convulsions from local affections of the nerves, and the traumatic tetanus from injury of a nerve.

Dr. Marshall Hall distinguishes four kinds of muscular contraction:

1. The voluntary, which appears to be dependent on the brain.

2. The respiratory, for which the nervous influence is apparently derived from the medulla oblongata. [With regard to these movements Dr. Hall has since altered his opinion.—See page 715.]

3. The involuntary, dependent merely on the nerves and muscles, and requiring the direct application of the stimulus to the muscles provided with nerves, or to the nerves of the muscles.

And, 4. The reflected muscular motion, which subsists in part after the voluntary and respiratory motions have ceased, and which is attached to the spinal cord, ceasing itself when this is removed, and leaving the irritability undiminished. The stimulus to the motions of this fourth kind does not originate in any central part of the nervous system, but at a distance from that centre: the motion is neither voluntary, nor direct in its course; on the contrary, it is excited by appropriate stimuli, which are not applied immediately to the muscular fibres and the motor nerves, but to certain membranous parts, from which the impression is communicated to the spinal cord. Dr. Hall illustrates the importance of this reflex function of the medulla oblongata and spinal cord by some examples. The prehension of the food by animals is an act of volition, and cannot be performed after the removal of the brain; the transit of the morsel over the glottis and through the pharynx is an act dependent on the reflex function, and is still capable of being exercised after the brain is removed. Although, in fact, the muscles which are called into action may be made to act by the influence of the will, yet the presence of the morsel in the fauces gives rise to a series of energetic movements (described at page 500); the stimulus of the morsel producing in the mucous membrane of the pharynx an impression, which, being communicated to the medulla oblongata, thus excites to action the motor nerves. Dr. Hall regards the further stage of the act of deglutition, in which the morsel is carried through the œsophagus, as the result of the irritability of this tube itself; which appears very doubtful.*

Dr. Hall proceeds to instance the permanent influence of the spinal cord on the sphincters. The sphincter ani remains firmly closed in a decapitated turtle as long as the lower part of the spinal cord is left uninjured; but immediately relaxes, and opens, on the spinal cord being withdrawn.

On the spinal cord being divided in a lively snake (coluber natrix) between the second and third vertebræ, the motions of the animal immediately ceased; and, while it was not irritated, it remained in a quiet state; but, on being irritated, it moved about for a considerable time; every change of position bringing new parts of its surface into contact with the ground. The animal by degrees became again quiet, but the slightest touch re-excited the motions.

Dr. Hall shows very beautifully the relation which exists between the voluntary, respiratory, and reflected movements; while, at the same time, he labours to prove that the reflected movements which occur after loss of the brain are not excited by true sensations, but only by the centripetal actions of the nerves, caused by the impressions on them.

* See page 657.

Sensation, volition, and motion are, he says, the three links of the chain, when motion is excited by pain; but if the middle one of these links is destroyed, the connection between the two others through the medium of the sensorium is at an end.

I agree with Dr. Hall as to the reflected motions which occur after the loss of the brain being no proof that stimuli applied to the skin are still able to excite true sensations in the spinal cord; the ordinary centripetal action of the nervous principle takes place in these cases, as when sensations are produced, but here it does not give rise to sensation, since it is not communicated to the brain, the organ of consciousness. During life, also, in the state of health, many reflected motions are excited by irritations of membranes, which are not, as true sensations, communicated to the sensorium, but nevertheless produce strong impressions on the spinal cord; as, for example, the irritation of the fæces or urine, exciting the contractions of the sphincters. But Dr. Hall goes too far in admitting that, in the healthy state, every motion which follows true sensation is voluntary, and that all irritations of sensitive parts which give rise to reflected motions are unattended with sensation; for the reflected motions of sneezing, coughing, and many others, are consequent on true sensations. The reflected motions, and the involuntary not reflected motions, must not be confounded with each other. If the glottis of an animal be touched, says Dr. Hall, it contracts; so, likewise, does the heart when touched. The removal of the brain does not affect these phenomena; but if the medulla oblongata be taken away, the larynx can no longer be made to contract, while the action of the heart continues even after the removal of the spinal cord. The heart is affected immediately on the application of any stimulus, by virtue of its "irritability;" the impression made by a stimulus applied to the larynx, on the contrary, must be propagated to the medulla oblongata, and the contraction is effected indirectly through the medium of the latter part. The head of a snake having been cut off, it was found that by touching any spot within the teeth of the lower jaw, or the openings of the nares, a movement of the larynx took place,—it was drawn downwards and closed. The phenomenon ceased on the medulla oblongata being removed. Dr. Marshall Hall mentions, lastly, as belonging to the reflex actions, the winking of the eyelids when they are touched; the peculiar effects of tickling, or of dashing cold water into the face, upon the respiration; sneezing from irritation of the mucous membrane of the nose; cough and vomiting from irritation of the larynx or pharynx; tenesmus from irritation of the rectum; and strangury from irritation of the bladder.

[Dr. Marshall Hall states, moreover, that muscles lose their tone,—become lax and flaccid, when the part of the spinal cord from which they receive their nerves is destroyed. He has observed, like our

author, that the tendency to reflex action in the nervous system is heightened in animals poisoned by strychnine and opium; and remarks that the tendency to this mode of action is equally depressed by the influence of hydrocyanic acid. Lastly, we may mention that Dr. Hall classes among the reflex phenomena all the movements of anencephalous monsters.]

We see that cramps occurring in diseased states may have very different sources. There are, namely, spasmodic affections of which the cause is seated in the motor nerves themselves, or in the brain and spinal cord: but convulsions also arise from reflex action of the nerves, their cause being irritation of sensitive nerves, of which we have instances frequently occurring in consequence of intestinal irritation, in dentition, odontalgia, and from painful affections of the nerves generally, whether these be dependent on organic lesions or not.

All the phenomena hitherto described agree in the circumstance of the spinal cord being the medium of communication between the centripetal nervous action produced by the exciting stimulus, and the subsequent motor action of the nerves; but the different "paths" of communication in the spinal cord may be more distinctly defined. The most common form of reflected motion is where violent impression on the sensitive nerves excites muscular contractions in the same limb; this is observed when the skin is burnt; and, in the first stage of narcotization of animal, a stimulus applied to the skin is prone to excite contractions in the same, rather than in other parts: thus, also, the stimulus of the morsel in the fauces excites the act of deglutition; dust on the conjunctiva, closure of the eyelids; and the irritation of the urine and fæces, the contraction of the sphincters. Hence we see that irritation propagated to the spinal cord most readily affects those motor nerves which arise nearest to the roots of the exciting sensitive nerves; in other words, that it is most prone to pass from the posterior roots, or the individual fibres of these roots, to the anterior root of the same nerve, like electricity, leaping by the most direct course from one pole to the other. To express it more correctly, and in the language of physiology, we may say that when the motor influence of the spinal cord is strongly excited by a sensitive nerve, that part only is at first affected which is nearest to the root of that nerve; and that the irritation of the cord, and of the motor nerves arising from it, diminishes in proportion with the distance from that point. In the same way, in the brain the irritation is communicated from certain sensitive to certain motor nerves; and there must be something connected with their original formation, which gives these nerves an especial tendency to reciprocal action. Thus, as we have shown, the optic and acoustic nerves, and the sensitive branches of the fifth nerve, are prone to excite reflex actions of the ciliary branches of the third pair and of

the facial nerve. [Mr. Mayo* seems to maintain that proximity of origin is a general condition when sentient and motor nerves are thus associated in their functions.]

The sensitive and motor nerves which thus react on each other through the medium of the brain and spinal cord, seem, as it were, to balance each other; one produces a change in the other, as one scale of a balance rising causes the other to descend, or as the sinking of a fluid in one branch of a bent tube makes it rise in the other.

Next to that just described, namely, the communication of the irritation from the sensitive nerves to the roots of the contiguous, or not far distant, motor nerves, the most frequent form of reflex action is the production of spasmodic contractions of the respiratory muscles from irritation of the mucous membranes. Hence there must pre-exist in the medulla oblongata and spinal cord some means of ready communication between the sensitive nerves of the mucous membranes (the fifth nerve in the nostrils; the vagus nerve in the trachea, lungs, pharynx, œsophagus, and stomach; the sympathetic nerve in the intestines and uterus; and branches of the sacral plexus and the sympathetic nerve in the urinary bladder and rectum,) on the one hand, and the motor nerves of the respiratory muscles (the facial, accessory, and spinal nerves,) on the other; while the spinal nerves which go to the extremities are excluded from this harmony of action.

In certain states of irritation of the spinal cord and brain, produced by the action of narcotic poisons, or other causes, however, every impression on a sensitive nerve is capable of exciting the spinal marrow to a discharge of motor influence by all the motor nerves, even by those which are least prone to be affected by reflex action,—namely, the motor nerves of the extremities. Volkmann has, indeed, shown that even dividing the spinal cord longitudinally in frogs previously decapitated does not prevent the extension of the reflex motions to all the muscles of the two halves of the body, so long as any portion of the spinal cord remains connected with the nerves.

We have, lastly, to inquire how far true sensation is engaged in the production of the reflex motions. Volkmann inclines to the opinion of Whytt, that the motions consequent on impressions are the result of sensations conveyed to the sensorium, giving rise to appropriate spontaneous reactions.

That this is in many instances the case, appears to me to be indubitable, particularly with those reflex phenomena which occur in an unimpaired state of the brain and spinal cord. Thus I regard, for example, the closure of the eyes under the stimulus of a strong light, and the action of the respiratory muscles induced by irritation of the mucous

* [See his observations on the origins of the cerebral nerves, at page 343 of his Outlines of Physiology. Second Edition. 1829.]

membranes of the respiratory organs, intestinal canal, or urinary system. But when we remember that, if we divide the trunk of a salamandra maculata into several portions, each part, if it contain a fragment of the spinal cord, will still evidence the reflex motions, we can scarcely maintain the applicability of this view to all cases.* The reflex phenomena are observed also to occur in parts withdrawn from the influence of the will, such as the intestinal canal and heart. The general spasms, lastly, which are excited by stimulus of a sensitive nerve in animals in a state of narcotization do not in the slightest degree resemble the phenomena of spontaneous reaction. The view which I take of the matter is the following:—irritation of sensitive fibres of a spinal nerve excites primarily a centripetal action of the nervous principle, conveying the impression to the spinal cord; if the centripetal action can then be continued to the sensorium commune, a true sensation is the result; if, on account of division of the spinal cord, it cannot be communicated to the sensorium, it still exerts its whole influence upon the spinal cord; in both cases, a reflex motor action may be the result. In the first case, the centripetal action excites, at the same time, sensation; in the latter case it does not, but is still adequate to the production of reflex motion, or centrifugal reflection.†

Dr. Hall's theory differs from that of Whytt, as well as from my own, and is peculiar. In the first place, he limits the phenomena of reflex action to the spinal nerves, and denies to the cerebral nerves of special sense the power of exciting them. He supposes the reflex motor actions to be in no case excited by sensation, nor even by means of the sensitive nervous fibres. He maintains the existence of special nerves, or nervous fibres, endowed with the "excito-motory" function; and the reflex action he supposes to be conveyed, not by the nerves of spontaneous motion, but by special fibres, which he calls "reflecto-motory."‡

* [Cases of paraplegia have been observed, in which involuntary retraction of the lower limbs could be excited by irritating the foot. (See Mr. Grainger's Observations on the Spinal Cord, p. 93; and Dr. Hall's Memoirs on the Nervous System.) The translator has now under his care, at the St. Pancras Infirmary, a woman aged 33 years, recently attacked with hemiplegia, (complete loss of sensation and motion in the left upper and lower extremity,) in whom, nevertheless, pinching, or even slightly touching the sole of the foot or ankle of the paralysed leg, causes the limb to be retracted and the toes extended, the patient being unconscious both of the stimulus and of the movement. The phenomenon is here the more striking, as in the opposite leg, which possesses its full voluntary power, no spasmodic contraction is produced, although the slightest touch is felt.]

† [Dr. Reid remarks that the sensations which attend some of the reflex motions have been added for an ulterior object—that it is necessary both for our comfort and well-being, that these movements (such as those by which the contents of the bladder and rectum are expelled) should be influenced by volition, and that this, of course, could only be accomplished by associating sensation with the excitation of the impression.]

‡ [Mr. Grainger conceives that he has discovered the hypothetical excito-motory nervous system of Dr. Hall, and its anatomy. Believing the grey substance to be the

The posterior roots of the spinal nerves, and nerves of the medulla oblongata, Dr. Hall teaches, contain sensitive and excito-motory fibres; the anterior roots, spontano-motory and reflecto-motory fibres; the vagus, too, he regards, not as a nerve of sensation chiefly, but as an excito-motory nerve; for, in an experiment performed by himself and Mr. Broughton, its division gave rise to no pain, but affected the movements of respiration. Dr. Hall has recently developed these views more fully.* Volkmann disputes their validity, and, among other arguments, states that Dr. Hall is incorrect in asserting the vagus to be insusceptible of painful sensations.

Volkmann points out a fact which we have ourselves often observed, namely, the great difference between the nerves themselves, and their peripheral termination, in the power of exciting reflex motions. No part equals the skin in the property of exciting reflex motions; the slightest touch applied to the surface, in animals in a state of narcotization, is frequently sufficient to give rise to strong spasms, while the reflex actions excited by irritation of the nerves themselves are much slighter.†

CHAPTER IV.

OF THE DIFFERENT ACTION OF THE SENSITIVE AND MOTOR NERVES.

Experience has taught us that, when a nerve is irritated at any point, the action of the nerve is manifested through its whole length; in a motor nerve exciting the contraction of muscles with which its fibres are connected, and in a sensitive nerve sensation, provided the fibres of the nerve be still in connection with the central organs of the nervous system. To explain this, it might be supposed that the effect of the irritation is propagated equally in both directions,—towards the peripheral extremity of the nerves, and towards its cerebral extremity: but it is equally con-

source of nervous power, and the white fibres mere conductors, he regards the grey matter of the cord as the central organ of the excito-motory system. And since part of the fibres of each root of the spinal nerves, as described by Bellingeri and Weber, (see the 2nd chapter of the 5th book,) pass inwards to this grey substance, while the rest of the fibres seem to be continued upwards to the brain, Mr. Grainger infers that the latter fibres are the conductors of volition and sensation; and that the former are the filaments which convey the incident impression and reflex influence on which the reflex phenomena depend. These views he supports by many ingenious but not conclusive arguments; he extends them also to the cerebral nerves. The optic nerve, for example, he believes to contain true sensiferous fibres, which are continued to the cerebral convolutions, and incident excito-motory fibres, attached either to the grey matter of the optic tubercles, or of the optic thalami; and hence he explains the fact proved by the experiments of Mr. Mayo and Flourens, that though, after the removal of the cerebral hemispheres in pigeons, vision is lost, the iris still acts under the influence of light, or when the optic nerve is irritated.—See Mr. Grainger's work on the Structure and Functions of the Spinal Cord.]

* Memoirs on the Nervous System.—London, 1837.

† [This fact was noticed by Dr. Whytt, and was adduced by him as an argument for the dependence of the sympathetic actions on peculiar sensations.]

ceivable that the irritation may be propagated in one direction only, namely,—in the fibres which excite motion, towards the brain; in those which excite sensation, towards the muscles. The latter was the view usually adopted before it was known that there are distinct motor and sensitive fibres. The question as to which supposition is correct, still presents itself; and its solution is of extreme importance in reference to the physiology of the nerves. *Is the nervous principle or force of the motor fibres different in its quality from that of the sensitive fibres? or are what are here called the motor and sensitive principles, actions of the same nervous principle, differing only in direction, being centrifugal in the motor, centripetal in the sensitive fibres?*

It is known that the action of motor nerves is propagated only in the direction of their ramification; that when a nerve is irritated, the muscles which receive branches from the nerve above the point of application of the stimulus are not thrown into contractions, while all the muscles are affected which are supplied from below the irritated part. From this fact it might be inferred that the action of the motor nerves is propagated in the centrifugal direction only. But there are other facts, according to which this may be explained differently. We know, from microscopic examinations of the nerves, that the primitive fibres do not unite with each other, but remain distinct from their origin to their termination; that the trunk of a nerve consequently is, as it were, the aggregate of all the fibres which are distributed in its branches. Hence, even if the motor nerves do propagate the nervous action in the centripetal as well as in the centrifugal direction, the irritation cannot affect the fibres of branches which come off from the stem at a higher point, but only those contained in the irritated branch, which are continued without being united with others even to the brain or spinal marrow. In the spinal marrow, too, this centripetal action of the motor fibres may remain insulated, if the fibres continue to be distinct there also; and, if they do not become united with sensitive fibres, no sensation will be excited in the brain or spinal cord. In the same way, the fact that irritation of sensitive fibres gives rise to no sensation, unless they are in connection with the brain and spinal cord, does not justify us in the conclusion that these fibres propagate nervous irritation in one direction only; for the opposite current, if it exists, cannot produce sensation, since it does not affect the nervous centre, the seat of perception.

If it were certain that the muscles possess contractile powers independently of the nerves, and that the nervous influence acts on them merely as other stimuli do,—that it is not necessary for other stimuli to act first upon the nerves before they can excite muscular contractions, then it might be shown that the sensitive fibres are capable of a centripetal action only; for I have observed that sensitive nervous fibres, even when they are distributed to muscles, as is the case

with the gustatory branch of the fifth nerve, which at all events forms anastomoses with the motor nerve of the tongue, (the ninth,) are still incapable of exciting contractions of those muscles. But the muscles have in fact no contractile power independent of reciprocal action with their nerves; they lose their irritability—their power of contracting on the application of all stimuli—when their nerves have long ceased to be in communication with the brain, and their power is lost in the same measure as that of their nerves: these facts are proved by the experiments performed by Dr. Sticker and myself. Now since the sensitive nerves, even when distributed to muscles, have no influence on them, it is evident that the reciprocal action which maintains the motor power in the muscles is carried on with the motor fibres only. But this again may with equal probability be ascribed to the motor nerves having a peculiar special property of their own; as, to their having alone the property of propagating nervous action in the centrifugal direction. I was very desirous of satisfying myself by experiment with regard to this extremely important point, and have discovered a means in the action of narcotic poisons by which at a future time the problem may be solved. We have already mentioned that, by poisoning with opium, such a state of irritation of the spinal cord in frogs, is produced, that the slightest shock, and even a local irritation propagated to the spinal cord, gives rise to general muscular spasms. The effect of the stimulus is here transmitted first to the spinal cord, which reacts upon all parts of the body; for parts separated from the trunk, and parts of which the nerves are divided, do not become convulsed. Now I wished to divide the posterior or sensitive roots of the nerves of the lower extremity in a frog, to poison the frog, and then ascertain whether irritation would be propagated in the centripetal direction by the nerves to the spinal cord, with which they communicated by means of the anterior roots, and whether irritation of a motor nerve in a limb devoid of sensation would give rise to general convulsions. The result of the experiment was in repeated trials opposed to such a view. The spasms did not take place when the irritation of the nerve was performed so as to produce not the slightest shock to the body of the frog; for example, when it consisted in dividing a nerve with scissors, or in irritating the nerve by means of needle and forceps. To perform the experiment well, the poison should be given first, and as soon as its effects begin to be manifested, as soon as a blow on the table on which the frog lies gives rise to slight convulsions, the spinal canal must be quickly opened, and the three posterior roots of the nerve of the posterior extremity divided on one side, while those of the other side are left uninjured; the ischiadic nerve should then be quickly dissected out, cut across above the knee, and left hanging from the thigh on both sides. The frog is then ready for the experiment. If the spinal canal be opened first, so much blood is lost that the

poison is not afterwards readily absorbed. The experiment is one of great difficulty, and requires to be frequently practised before it can be performed satisfactorily. The poison must not be given in too large quantity, otherwise paralysis will ensue too rapidly. Opium is best; nux vomica induces paralysis too soon. The frog being prepared as just directed, cut off with a pair of scissors a portion of the nerve on the side on which the posterior roots are divided, in such a manner as to produce no shock to the body of the animal. No convulsions will ensue. Cut in the same way a piece from the extremity of the nerve of the opposite side, which still communicates by its sensitive roots with the spinal cords, and a convulsion of the whole frog is each time produced. If the experiment was performed awkwardly, so that in cutting the nerve a shock was communicated to the body of the frog, and thence to the spinal cord, general spasms were produced, even in cutting a portion from the nerve on which the sensitive roots had been divided; but here the shock was the cause of the phenomenon, as is proved by the circumstance that, even after division of the nerve, a twitching motion applied to the leg so as to affect the body was sufficient to produce the same effect. I have devised the following experiment likewise as a means of solving the problem, but have not yet performed it.

We have already seen that the motions of the iris on the two sides are always simultaneous, and that the application of the stimulus to one eye is adequate to produce contraction of both pupils. It is also known that the light does not act immediately on the iris, but on the retina, and that the contraction of the iris is the result of a reflex action from the brain; for the iris of an amaurotic eye, which is itself insensible to light, contracts when the light acts upon the sound eye. Now Mayo has shown that the third or motor oculi nerve is the motor nerve of the iris. Will then irritation applied to the third nerve on one side be propagated by the nerve backwards to the brain, as the optic nerve does, and excite contraction of the iris on the other side? The value of this experiment, however, rests upon the supposition, which is by no means probable, that the third nerve contains no sensitive fibres.

The second part of the question, namely, whether the nervous action in the sensitive nerves follows the centripetal course only, and not the centrifugal, from the brain and spinal cord, might be decided in the affirmative in so far as all sensations are attended with centripetal action. There are, however, also sensations excited by passions or imaginations of the mind, which appear to be propagated from the spinal cord through the whole length of the nerves, even as far as the toes. But here again another explanation may be adopted. We have shown that the sensitive fibres of all parts of a nerve are contained in the trunk of the nerve and in its roots, and that pressure on the nerve itself excites the same sensations as if all its branches were affected.

When, therefore, the roots of the nerves of a limb communicate by centripetal action an impression to the spinal cord, the sensations must necessarily be felt in the limb. When further, any cause, such as terror, produces a sudden change in the state of the sensitive force of the spinal cord, the fibres of the sensitive roots of the nerves will make a different impression from that which they previously made, and in consequence sensations will be felt in the limbs.

The affection of the nervus lachrymalis, under the influence of certain passions and ideas, is apparently an instance of the transmission of nervous influence in a centrifugal direction in a decidedly sensitive nerve; and this would be a decisive proof that sensitive nerves can propagate nervous action in the centrifugal direction, if it were certain that the lachrymal nerve is not, like other branches of the fifth nerve, accompanied by branches of the sympathetic. But it is probable that the lachrymal nerve receives grey fibres, since the entire first division of the fifth nerve receives them, as we have already shown.

The fact, too, that other nerves which serve principally for sensation, for example, the nervus vagus, have an evident organic influence on nutrition and secretion, and even on motion, might be explained in the same manner. The nervus vagus in many animals, as Professor E. H. Weber has shown, even supplies in great part the place of the sympathetic; this is the case in snakes, for instance, where it is distributed to a great part of the alimentary canal. In the myxinoid fishes the vagus extends as far as the anus, and the sympathetic nerve is absent. Since then the sympathetic and the vagus nerves mutually replace each other, and since the extent of the distribution of the one determines the limits of the distribution of the other, it might appear to be demonstrated that other than retrograde currents or vibrations can be propagated in a sensitive nerve. This argument, however, is of no great weight; for the organic actions of the vagus are most probably owing to its containing organic fibres derived from the sympathetic nerve, with which it has such frequent communications. Throughout the system, the fibres which constitute a nerve, after it has passed a certain extent of its course, are very different from those which it has at its origin: many other fibres of very different nature becoming associated with it. We have a very evident example of the super-addition of organic fibres to a motor nerve, and a proof of the great difference there must be between organic and motor nervous actions, in the case of the nervus buccinatorius of the ox, which receives from the otic ganglion a fasciculus of grey fibres that accompany it, probably to be distributed in the mucous membrane of the mouth and glands of the cheek. Here we see that for the motor and organic influences different conductors are necessary: we have the same proofs in the case of sensitive nerves.

The fact that the nerves of the different senses, when affected by the

same stimulus, become each the seat of its peculiar sensation,—the mechanical or galvanic stimulus exciting in the optic nerve the sensation of light, in the auditory nerve that of sound, and in the nerves of touch that of pain,—cannot be adduced in favour of either hypothesis; for it is explicable as well on the supposition that the forces of the different nerves are different, as on that of the different sensations arising from centripetal actions of the same forces being transmitted to different parts of the brain. It is remarkable, however, that many stimuli act only on particular nerves. Thus, light affects only the optic nerves, and, as a warming agent, the nerves of touch, but no other nerves; and the olfactory nerve would appear to become the seat of smell, under the influence of no other stimuli than odoriferous substances and electricity.

However this may be, it is certainly not satisfactorily proved that the sensitive fibres are capable of centripetal action only, and the motor fibres only of centrifugal. There is one circumstance, in particular, which excites still greater attention in reference to this subject. It is the fact noticed at page 632, that for the preservation of the excitability of the motor nerves their communication with the central organs of the nervous system is necessary: this is in appearance in favour of all nerves, including the sensitive nerves, being equally dependent on the brain and spinal cord; in which case, however, there would be centrifugal emanations from the latter organs through the sensitive nerves. Future experiments founded on well conceived ideas or new discoveries must decide the question; and we can, at present, only congratulate ourselves that the investigation of this important problem, on the decision of which so many others depend, has by the observations above detailed been at least introduced into the province of experimental physiology.

If this first question cannot be decided, still less can it be proved that the centripetal and centrifugal conductors form a continuous circle in which a constant current of the nervous fluid is kept up from the central organs through the motor nerves, and from the peripheral extremities of these through the sensitive nerves back to the central organs. It might be imagined that life is constantly attended with a circulation of the nervous fluid, which would be capable of being reduced only to such a low degree of activity as would give rise to the imperceptible constant play of the muscular fibres in the state of apparent rest,—the antagonistic action of the different muscles; and the indistinct feeling by which a healthy person is made conscious of the existence of the different parts of his body. The hypothesis of the circulation of the nervous fluid, or of its vibrations in the two kinds of nervous conductors, is, however, for several reasons very improbable; for, since many nerves are sensitive only, these must either not be the seat of a circulation, or we must suppose again that with their

sensitive fibres they contain an equal number of fibres of centrifugal action, which do not give rise to motions, only because they do not terminate in muscles. Now, if we merely regard those motor and sensitive nerves which communicate by anastomoses of their fasciculi, as in the instance of the facial and infra-orbital nerves, still less can we find in them the means for a circulation of the nervous fluid: for, in the first place, these anastomoses are not real communications of the primitive fibres; and secondly, an irritation excited in the facial nerve is proved by the experiments of Gaedechens (see page 660) not to be communicated through these anastomoses to the trunk of the infra-orbital nerve so as to excite pain. All these considerations teach us that the existence of a regular circulation of the nervous fluid from the brain and spinal cord through the nerves back to the central organs cannot be demonstrated, and in the present state of our knowledge appears very improbable.

CHAPTER V.

OF THE LAWS OF ACTION OF THE SYMPATHETIC NERVE, AND THE PROPAGATION OF IMPRESSIONS IN IT.

Our knowledge of the mechanical laws according to which the sympathetic nerve acts, is still extremely incomplete: in this department of physiology little more has been done than to propose certain hypotheses, none of which can be either proved or decisively refuted. The only way in which we can arrive at some accurate knowledge on the subject, is to compare with the phenomena presented by the sympathetic nerve, the facts which are ascertained with regard to the action of the cerebro-spinal nerves, and to investigate by new observations how far the mode of action of the sympathetic differs from that of other nerves. We have to inquire, therefore, whether the fibres of the sympathetic are, like those of the cerebro-spinal nerves, insulated in their action, or whether they can impart their influence to each other; whether the radiation of the motor influence, and the coincidence or confusion of different impressions, is not the normal mode of action in this nerve; whether the ganglia are multiplicators of the nervous influence, and as it were small independent nervous centres or points of radiation; whether there is not in these ganglia a reflection of the nervous influence in certain directions; whether the ganglia are the cause of the indistinct and vague character of the sensations in the sympathetic; whether they are the organs on which the radiation or confusion of sensations depend, or whether they are imperfect conductors which impede the transmission of impressions to the brain and spinal cord, and of the influence of the will to the parts supplied by the sympathetic; or whether they are not rather the central parts from which the organic influence of the sympathetic emanates for the regulation of the organic chemi-

cal processes; lastly, whether the impressions are propagated from an irritated point in the centripetal or the centrifugal direction, or in all directions. It is to be lamented that none of these questions admit at present of a decisive answer. Of the few facts that we know with certainty with regard to the action of the sympathetic nerve, part only have relation to these questions; and of the hypotheses respecting the uses of the ganglia especially, not one can be definitely proved or refuted.

The lateral main cord of the sympathetic is indubitably of importance to the whole sympathetic system, inasmuch as in it the radicle fibres of the sympathetic derived from the cerebral and spinal nerves are collected preparatory to their further distribution; the individual cords of communication between the ganglia, however, do not appear to be absolutely necessary for the performance of the function of the sympathetic; at all events, M. V. Pommer's experiments on animals have shown that the sympathetic may be divided between the first and second cervical ganglion on both sides without any remarkable consequence ensuing within the space of seven or eight weeks, which was the period during which the animals were watched.* This shows, at the same time, that the cephalic portion of the sympathetic may be isolated from the thoracic portion without any injury to life, the inferior cervical ganglion and the thoracic portion of the sympathetic receiving the nervous influence from the central organs of the nervous system in a greater degree through the medium of the spinal nerves, with which they are connected, than from the cerebral nerves.

a. Of the actions of the sympathetic nerve in involuntary motions.

I. *All the parts subject to the influence of the sympathetic nerve are incapable of voluntary motion.*—The heart, the intestinal canal, the efferent ducts of glands, the uterus, and the vesiculæ seminales, afford proofs of this statement. It appears, indeed, on the first view, that a cerebrospinal nerve, when it has numerous communications with the sympathetic, loses its voluntary power; as an instance of this, the lower part of the vagus might be adduced. The motions of the œsophagus are involuntary, although those of the pharynx are subject to the will. It is doubtful, however, whether the motor nerves of the œsophagus be derived from the vagus itself (see page 657). The urinary bladder receives nerves of two kinds,—branches from the sacral plexus, and others from the hypogastric plexus of the sympathetic. This agrees with its observed functions. The influence of the will over the bladder is very slight.

On the other hand, all muscles which receive nerves from the cerebrospinal system only are capable of voluntary motion. The small muscles of the ear, in some individuals at least, as in myself, can be moved voluntarily. The cremaster, a prolongation of the obliquus internus

* V. Pommer, Beiträge zur Natur und Heil-kunde. Heilbronn 1831.

and transversus abdominis muscles, can likewise be made to act voluntarily in some persons, although very many persons have no power over it.

II. *The parts which are supplied with motor power by the sympathetic nerve still continue to move, though more feebly than before, when they are separated from their natural connections with the rest of the sympathetic system, and wholly removed from the body.*—Thus the heart, after it is taken from the body, continues to beat for a considerable time,—in reptiles and amphibia for hours; the peristaltic motions of the intestines continue under the same circumstances. The separated oviduct of a turtle has been seen to contract and expel its contents.

III. *Hence all the parts endowed with motion, and supplied with nerves from the sympathetic, are, in a certain degree, independent of the brain and spinal cord.*—The extent to which this is the case has been investigated at page 192. We may mention here as a principal result, that not merely the heart continues to beat feebly for a long period after the destruction of the brain and spinal cord, but that there are well confirmed accounts of embryos in which the brain as well as the spinal cord have been slowly destroyed by disease during the life of the fœtus.*

IV. *The central organs of the nervous system can, however, exert an active influence on the sympathetic nerves and their motor power.*—It results from the experiments of Dr. Wilson Philip and others, detailed at page 194, that the motions of the parts supplied with nervous influence by the sympathetic do not immediately cease on the sudden destruction of the brain and spinal cord; but that, nevertheless, the character and rapidity of the heart's beat may be influenced by inflicting injury or irritation on the brain and spinal cord previously in an unimpaired state: thus, Dr. Philip states, that, by dropping alcohol and infusion of tobacco upon the brain of animals, he has caused acceleration of the motion of the heart. The influence of the passions is much more evident.

V. *The experiments of Dr. Philip tend to show, also, that distinct parts of the brain and spinal cord do not alone influence distinct parts of the sympathetic system, and of the motions dependent on it; but that the brain and the whole spinal cord, or every part of it, can exert an influence on the motions of the heart.*—Irritation of certain parts of the spinal cord gives rise primarily to motions of certain voluntary muscles only—to those which receive their nerves from the irritated part; while, in the production of involuntary motions, every part of the spinal cord appears to have alike the power of influencing the sympathetic nerves. This difference, the existence of which, however, is not at present sufficiently established, might be explained in two ways; either the spinal cord, or the ganglionic nerves themselves, might be regarded as the cause of the diffusion of the influence. In the first case, the fibres of the gan-

* See page 197; and Eschricht, über Gesichts-verdoppelung mit Mangel von Gehirn und Rückenmark. Müller's Archiv. 1834, p. 268.

glionic nerves sent to the heart would have no reciprocal action with the nervous fibres of other parts; the extension of the influence would take place in the spinal cord itself, the nervous fibres of the different parts being in the cord itself determined to sympathetic actions. According to the second explanation, the ganglia would be regarded as the cause of the phenomenon. We must confess, that no direct experiments, of a satisfactory nature, have as yet been instituted in relation to this important question.

Having divided the splanchnic nerve in a rabbit, I laid the end of the distal portion on an insulating plate of glass, and galvanised it by means of a battery of sixty-five pairs of plates. Increased peristaltic movements of the intestines ensued, whence might be inferred that this nerve exerts an influence on the whole intestinal canal, and not on one distinct portion of it. The result was the same from the application of caustic potash to the cœliac ganglion in a rabbit, in which the intestines were laid bare, and in which the increased peristaltic movements excited by the first exposure to the air had again subsided and become very feeble; the movements were, on the application of the potash, immediately rendered very lively.

VI. *The movements excited in organs which are under the influence of the sympathetic nerve, by irritation applied to them or to their nerves, are not transitory and momentary contractions; they are either more enduring contractions, or they consist of a long-continued modification of the ordinary rhythmic action of the organ: hence, in these organs, the reaction consequent on the irritation is decidedly of longer duration than the action of the stimulus.*—The motion of the nervous principle in the sympathetic nerve then is slow, and its rate capable of being measured. The abdomen of an animal being laid open, if the intestine be irritated at any point either by a chemical or mechanical stimulus, or by galvanism, contraction of the intestine ensues very gradually, and frequently attains its greatest degree when the exciting cause has long ceased to act. The same takes place in the heart in a different manner: instead of a persistent, not periodic contraction, the momentary application of a stimulus to the heart excites a continued series of periodic beats. The action of the heart can be excited both by mechanical and by the galvanic stimulus. Contraction has been produced both by Humboldt and myself in the heart of the frog by means of galvanism; the galvanic stimulus does not, however, always cause an instantaneous contraction of the heart, but frequently causes merely a change in the number and rapidity of the succeeding beats. The mechanical stimulus also applied to a heart acting slowly, does not always excite an immediate contraction; this frequently follows after the lapse of several seconds: the effect is, however, evident, as we see when the heart of a frog which is cut from the body, and which has ceased for some time to beat, is irritated. In

the case of the heart, therefore, as with the intestinal canal, the reaction frequently does not become evident till some time after the application of the stimulus, and continues longer than the action of the latter. But what distinguishes the heart is, that a temporary stimulus does not excite a continued contraction, as in the intestine, ductus choledochus or sphincter vesicæ, but produces changes in a whole series of successive pulsations. If a heart has been beating for a considerable period every four or five seconds, the application of a temporary stimulus causes it to beat for a long time at a different rate, namely, every second, or every two seconds; and if it has wholly ceased to beat, the stimulus causes it to contract, not once merely, but many times, within a certain period. The effect is the same when the stimuli are applied, not to the muscles themselves, but to the sympathetic nerve. Humboldt and Burdach have observed, that, on applying galvanism to the great cardiac nerve in a living animal, the pulsations of the heart, which had become slow, were quickened; the new type of the pulsations thus excited continuing after the stimulus had ceased to act. In the experiment already mentioned, in which I irritated the splanchnic nerve in a rabbit, the increased peristaltic motion of all the intestines continued for a very long time after the irritation, which was only of short duration, had ceased.

VII. *The final cause of the involuntary motions, and the cause of their type, lies neither in the brain nor in the spinal cord, but in the sympathetic nerve itself; even the influence of the ganglia is not necessary; the branches of the sympathetic going to an organ may be entirely removed, the twigs distributed to the substance of the organ only being left, and the motions will be maintained as before, the reciprocal action between the muscular fibres and these ultimate nervous twigs being apparently adequate to their production.*—It is a well-known fact, that the heart removed from the body of an animal, and emptied of blood, continues to contract rhythmically in the frog for several hours; this alone proves that the cause of the rhythm of its contractions cannot be the alternate influx and expulsion of the blood, but must reside in the organ itself. Now, since in all other organs capable of motion the action of the muscle always depends on its innervation, and since the contractile power of the muscle is lost in the same degree as the excitability of the nerves declines, (see page 632,) it follows that the final cause of the motions of the ventricles and auricles, and of their rhythm, as well as of the alternating peristaltic movements of the intestines, must be the reciprocal action going on between the sympathetic nerves and the muscle, an emanation of the nervous principle of the sympathetic acting periodically. It might be conceived that the action of the nerves is constant, though the muscle reacts periodically, the susceptibility of the muscles for the influence of the nervous principle being modified by every contraction: but this explanation would certainly be incorrect; for there is no apparent reason

why the heart should at each moment lose and again recover its susceptibility for the stimulus of a constant current of the nervous principle, while the voluntary muscles preserve their susceptibility for a continuous current so long as in the long-continued muscular actions.

The fact that the type of the rhythmic or peristaltic movements is continued in the parts endowed with involuntary motion, even when removed from the body, proves clearly that this type is independent of the brain and spinal cord; we have just shown that its cause lies in the sympathetic nerve itself. It remains for us to prove the second part of the above statement, namely, that the trunks and ganglia of the sympathetic are likewise not necessary for the maintenance of the type of the involuntary movements, but that even the ultimate ramifications of the nerve are still capable of yielding the necessary influence. The trunks of the cardiac nerves are not necessary for the maintenance of the heart's contractions; the heart of a frog continues to beat with its ordinary rhythm even when the entire base of the organ, when the auricles, as far as their juncture with the ventricles, are cut away. In the same way the peristaltic movements of the intestinal canal continue, not only when the intestine is removed from the trunk, together with the mesentery and ganglionic plexus, but also when the intestine itself is isolated from the plexus, by being separated from the mesentery at the line of insertion of the latter. In these cases the peripheral ramifications of the sympathetic in the substance of the heart and intestine are alone retained, and nevertheless these organs continue to move in their ordinary manner for a considerable period.

VIII. *Although from the foregoing observations it is certain that the extreme minute branches of the sympathetic have still the power of regulating the movements of the parts not subject to the will, yet it is not less true that both the brain and spinal cord, and the ganglia themselves, when in a state of irritation, exert an influence on these movements as long as the organs which are the seat of these movements are connected with them through the medium of the nerves. The brain and spinal cord are, however, also to be regarded as the source of the power of the sympathetic itself, which would without them become exhausted.*—We know that every passion of the mind affects the heart's action, and the motions of the intestines are modified by irritation of the spinal cord. In paralytic affections of the spinal cord, again, the movements of the intestines become sluggish. Irritation of the ganglia themselves likewise affects all the nerves which issue from them to be distributed to parts endowed with involuntary motion; this is proved by the following experiments. I have already mentioned that by applying galvanism to that portion of a divided splanchnic nerve in a rabbit which was connected with the cœliac ganglion, the nerve lying on a plate of glass, I succeeded in causing increased peristaltic action of the whole intestinal canal. It might be objected to this experiment,

that the galvanic battery, consisting of sixty-five pairs of plates, was much too powerful, and that the galvanic current might on that account have been conducted by the surrounding moist tissues to the intestines themselves. But I have performed other experiments, the results of which are quite decisive. I laid bare in a rabbit the whole intestinal canal, and at the same time the cœliac ganglion. As soon as the intestines of an animal are exposed to the action of the air, their motions become much accelerated; this continues for a considerable time, and then gradually subsides, until the peristaltic movements become very faint. I waited till this was the case, and then touched the cœliac ganglion with a piece cf caustic potash, when immediately the peristaltic movements again became very vigorous. I repeated this experiment, and obtained the same unequivocal result.

IX. *It results from the facts already stated, that the sympathetic nerve is charged as it were with nervous power by the brain and spinal cord, which may be regarded as the sources of nervous influence; but that, when once charged, it continues to emit this influence in the manner peculiar to itself, even when the further supply is for a time diminished. This affords an explanation for a part of the phenomena of sleep.*—While the sensorium commune falls for the most part into a state of inaction during sleep, the motion of the heart, and that of the intestines, continue with little or no change; for the organs supplied by the sympathetic nerve are independent of a partial and temporary rest of the sensorium, as long as they are charged as it were with nervous energy. The nervous principle seems indeed to be the more directed from the central organs towards the sympathetic part of the nervous system during sleep, in proportion as it is less required in the performance of the mental functions and the action of the organs of the senses. In syncope the action of the heart becomes faint, it is true; but it is much less depressed than that of parts under the influence of cerebro-spinal nerves. Here there is manifested the same phenomenon as is observed for a certain time, only in a less degree, in the heart and intestine cut from the body of an animal. If, however, the power of the brain and nervous system to afford nervous energy be too much depressed, if the supply of power to the sympathetic even at long intervals be arrested, the nerve falls into the state of exhaustion in which the cerebro-spinal nerves are involved each day, namely, during sleep; and a condition which cannot be removed by a further supply of nervous energy then ensues; hence the frequent feeble and scarcely perceptible pulse which proclaims the approach of death at the termination of acute diseases.*

X. *The influence of narcotics locally applied to the sympathetic nerve does not extend to the distant organs which the nerve supplies; but these organs may be paralysed by the direct narcotisation of the minute*

* Compare Dr. Wilson Philip's Observations on Sleep, Philos. Trans. 1833.

nervous fibrils which are distributed in them.—In this respect the sympathetic resembles the cerebro-spinal nerves, which are affected by a narcotic substance, and deprived of their excitability, only so far as the substance has actually touched them. But with reference to the action of narcotics on the organs under the influence of the sympathetic, there is observed in the case of the heart a remarkable, and at present inexplicable difference between the external and internal surface of the organ. If a narcotic, such as pure opium, or extract of nux vomica, be applied to the external surface of the heart, it produces little or no effect, or, at all events, a very slow one; the rhythmic motions of the heart of the frog, removed from the body and thus treated, continue for a very long time; but if a small quantity of opium or extract of nux vomica be brought into contact with the inner wall of the ventrîcle, its movements are permanently arrested, frequently in a few seconds after the application of the poison. Of this fact, first observed by Dr. Henry,* I have satisfied myself by repeated experiments on frogs. It is another proof that the motor power of the muscles is dependent on a reciprocal action between them and the nerves, and not a property of the muscular substance alone. Here the application of narcotics to the exterior layer of the heart's substance does not readily paralyse it, while, by applying the poison to the inner surface, the outer layer of the organ is immediately deprived of its power together with the inner layer; a circumstance which cannot be accounted for by any property of the muscular substance, but must be owing to an action on the nervous fibres. The rapid effect of the poison is likewise not explicable on the supposition that the poison penetrates from within rapidly through the walls of the heart; for when the auricles of the frog's heart are wholly removed, as in my experiments, and a little poison introduced into the open ventricle, it would rather be expelled again by the next contraction than received farther into the structure of the organ, which moreover could not be effected by means of vessels. The remarkable observation here detailed explains, however, the rapidity of narcotic poisoning, when the poison has once entered the blood and reached the heart.

XI. *The laws of reflection stated in the third chapter of this section prevail likewise in the actions of the sympathetic nerve; strong impressions on parts supplied by the sympathetic nerve may be propagated to the spinal cord, and give rise to motions of parts which derive their nerves from the cerebro-spinal system.*—Thus the convulsions in children, from intestinal irritation, are produced by the irritation being communicated to the spinal cord, and thence reflected upon cerebro-spinal nerves. Hence, likewise, the spasmodic action of the respiratory muscles in the vomiting excited by irritation in the intestinal canal, in the kidneys, in the

* Edinb. Med. and Surg. Journ. 1832.

uterus, or other organs. All spasmodic affections arising from local affections of the abdominal viscera are produced in the same manner. This reflex action from irritation of the sympathetic nerve can be proved experimentally; I have excited contractions of the abdominal muscles by irritating the splanchnic nerve; and Volkmann has observed convulsions of the body produced by irritating the intestines in decapitated frogs.

XII. *Impressions on parts of which the nerves are derived from the sympathetic are communicated to the spinal cord and brain, and excite the motor influence of the sympathetic nerve by reflection, although the reflex action is here less marked than in the case of the cerebro-spinal nerves.*—We have an instance of this in the frequent necessity to pass the urine, or the contraction of the bladder when the urine is of an irritating quality; for in this case the irritant does not act immediately on the muscular coat of the bladder, but in the first place upon the sensitive nerves of the mucous membrane. The variations in the size of the pupil from different affections of the intestinal canal, and the altered action of the heart in diseases of the abdominal viscera, are also instances of reflected nervous action. All such phenomena have been attributed to a sympathetic action of the sympathetic nerve itself, independently of the brain and spinal cord; but as in the cerebro-spinal system the sensitive impressions cannot produce the reflected motions except through the medium of the brain and spinal cord, so it appears *à priori* more probable that the reflected actions of the sympathetic are effected through the medium of the great central organs of the nervous system. When we compare the reflex phenomena presented by the cerebro-spinal nerves with those in which both the original excitation and reflected action are seated in parts under the influence of the sympathetic, we find that the former are much more energetic and readily excited than the latter; for how frequent, rapid, and easily induced are the reflex motions of coughing, sneezing, vomiting, &c.; how much more numerous are the reflex phenomena in the cerebro-spinal system, compared with those presented by the organs governed by the sympathetic. The circumstance, also, that inflammations of the intestinal canal do not affect the pulse,—that is, the heart's action,—so quickly nor to so great a degree as inflammation of other parts supplied with cerebro-spinal nerves, seems to favour the opinion that reflex motor action of the sympathetic nerve is less readily excited by irritation of the sympathetic itself than through the medium of the cerebro-spinal nerves; or rather, perhaps, that circumstance is elucidated by the latter fact.

It is difficult to institute experiments on this point of inquiry, and those which I have performed do not show that there is any particular tendency to reflex action in the sympathetic itself. I laid bare the intestinal canal of a living rabbit, and irritated it strongly by applying a

ligature tightly around it at one point of the small intestine. I then replaced it in the abdomen. I wished to ascertain whether this would excite by reflected action from the spinal cord a contracted state of the intestine for any distance on each side of the ligature. No such effect was produced; nor was I more successful on a repetition of the experiment. Volkmann's experiments, however, show that in a frog, which is in the peculiar state of predisposition to reflex action produced by decapitation, a reaction of the kind just mentioned can be produced. By pinching the intestine Volkmann could excite contraction of its coats, not at the irritated point merely, but for a more or less considerable extent; sometimes above, sometimes below the seat of the irritation. After destruction of the spinal cord, the part pinched alone contracted.

XIII. *Reflected action of the sympathetic, from an impression communicated to the spinal cord by cerebro-spinal nerves, is a more frequent occurrence.*—As instances of this we may mention the effects on the heart's action of strong pleasurable or painful sensations of the skin; the movement of the iris from impressions on the optic, auditory, and fifth nerves (see page 712); and the contraction of the seminal vesicles from irritation of the sensitive nerves of the penis.

XIV.—*Can reflex phenomena be produced in the sympathetic nerve through the influence of the ganglia, and independently of the brain and spinal cord?*—This interesting question cannot at present be decided. If such a mode of reflex action existed, it would constitute a remarkable difference between the sympathetic and the cerebro-spinal nerves; and, by means of their ganglia, the primitive fibres would be enabled to act on each other, which in the cerebro-spinal system never occurs, except through the medium of the brain and spinal cord. If muscles which derive their nerves from the cerebro-spinal system, and which are separated from the trunk of the body, be irritated, neither the whole muscle, nor even the entire length of a muscular fibre, contracts, but merely the part directly affected by the irritation. The question is, therefore, whether on irritating a single point of the intestines removed from the living animal, together with the mesentery and ganglionic plexuses, contractions of some extent, as, for example, of an entire loop of intestine, will take place. It will not. On the contrary, the irritated part only will contract; indeed, on pinching the intestine with forceps, there does not even follow a circular contraction of the whole tube, but merely a very limited contraction at the part pinched, while the opposite side of the canal remains quite flat and undisturbed. I have observed this fact repeatedly with reference to the intestinal canal, and once also I have made the experiment on the uterus of a pregnant rabbit. The muscular fibres immediately surrounding the part irritated became hard and contracted, but the rest of the uterus remained unaffected.

Volkmann has repeated this experiment on frogs with the same result. Hence he denies that the ganglia have the power of giving rise to reflected motions. He lays stress particularly on his experiments on frogs, which by decapitation had acquired the tendency to reflex action. As long as the spinal cord was present, pinching the gut at one point gave rise to contractions of great extent, but after the cord had been destroyed, the reaction was limited to the irritated spot.

As to the heart, the question is attended with more difficulty. It would appear that, in a heart separated from its connections with the rest of the body, the irritation of a single point could be propagated to the whole organ. If the heart of a frog be cut out and left undisturbed until the frequency of its beats shall have so far diminished that considerable intervals intervene between the contractions, which is the proper period for experiments on its irritability, mechanical irritation by means of a needle excites a contraction which cannot be confounded with the regular beats; and it is very remarkable that, at whatever part the irritation be applied, the reaction is the same as if the whole heart had been irritated,—that is to say, there ensues a contraction not at one point only, but of the whole organ. From this it would appear that in the heart, the local change in the irritability produced by the mechanical stimulus is propagated through the whole substance of the organ. The proper explanation of the phenomenon is not at present quite evident. The ganglia can have no share in its production, since it occurs in a heart perfectly freed from surrounding parts. The mechanical shock may perhaps contribute to the extension of the movement.

XV. *We are at present entirely ignorant as to whether irritation in one organ can, through the medium of the sympathetic, give rise to sympathetic movements in another;* since all the sympathetic phenomena of this kind can be explained on the principle of reflection from the brain and spinal cord.

XVI. *It is not proved, (and several facts have been observed which are opposed to the belief,) that the ganglia can exert an insulating action so as to impede the transmission of motor influence from the brain and spinal cord.*—I may remark that it is not voluntary influence, but motor influence generally, which is here referred to. Every one is aware how readily and quickly an impression on the brain and spinal cord influences the whole sympathetic system, how quickly a mental emotion alters the heart's action, and gives rise to movements of the intestines together with borborygmi; how a hysterical fit, in which the central organs of the nervous system are affected, terminates with a rumbling of air in the intestines. We shall presently see that the ganglia are likewise not capable of impeding the transmission of the retrograde or centripetal actions of the sympathetic nerve. The motor influence of the central organs of the nervous system, however, when exerted upon the sym-

pathetic nerve, does not give rise to rapid contractions corresponding in duration to that of the exciting stimulus such as result from its action on cerebro-spinal nerves, but rather alters the condition or "modus" of a continued series of contractions. But this power of modifying the effects of impressions made upon parts supplied by the sympathetic nerve is not a property of the ganglia only; it is possessed by the whole sympathetic nerve, and even by its smaller branches: for by irritating momentarily the heart of an animal removed from the body, already become feeble in its action, the character of its pulsations may be made to undergo a change of considerable duration; and the effect of a stimulus applied to the intestines removed from the abdomen lasts long after its application, and does not immediately attain its greatest degree.

XVII. *It is not certain that the ganglia are the cause of the parts supplied by the sympathetic nerve being withdrawn from the influence of the will.*—No proof of the truth of this statement need be adduced, since we know of no satisfactory arguments in favour of the contrary view. I must, however, remark that it is much more probable that the ganglia are *not* the cause of the arrest of the current of voluntary influence to these parts; for, inasmuch as they do not prevent the transmission of motor influence generally, which we have already shown that they do not, there is no reason why a voluntary motor influence should be arrested by them. It appears, therefore, that the cause of the parts of which we are speaking being withdrawn from the influence of volition does not lie in the sympathetic nerve and its ganglia, but that the peculiarity depends on the fibres of the sympathetic in the spinal cord and brain not being, like the fibres of other nerves, brought into communication with the source of the voluntary influence. The parts of the body, therefore, which are under the influence of the sympathetic, are, in respect of the want of voluntary power, in some measure comparable to the parts which are naturally endued with voluntary power of motion, but in which this power is paralysed. In this case, the current of motor influence determined by the will towards a nerve may be interrupted at any point of the spinal cord, and nevertheless the nerve will still be susceptible of the involuntary motor influence of the portion of the cord situated below the seat of injury.

XVIII. *In certain organs, which are subject to the influence of the sympathetic and of the spinal nerves at the same time, a voluntary influence seems to be exerted only after the long continuance of a centripetal or sensitive impression.*—The urinary bladder presents this phenomenon. The relation in which this organ stands to the brain and spinal cord is very enigmatical. It receives nerves entirely of the sympathetic nature from the hypogastric plexus; and also nerves not of this system, namely, branches from the sacral nerves. It appears to be, under ordinary cir-

cumstances, wholly withdrawn from the influence of the will; and nevertheless, when distended, we are able merely by a voluntary effort, and without any aid from the diaphragm and abdominal muscles, to expel the urine. E. H. Weber* likewise admits that the bladder is in some degree subject to the influence of the will. However, this power does not come into operation until a considerable accumulation of urine has taken place; in other words, not until this fluid has made a long-continued impression on the sensitive nerves of the bladder, and through the medium of them upon the spinal cord.

XIX. *Many parts which are supplied by the sympathetic nerve are indeed capable of involuntary motion only, but become associated with the motions of parts subject to volition, a part of the voluntary motor influence being communicated involuntarily to them, just as in the associate motions of voluntary muscles.*—Of this an example is afforded by the iris. It is difficult to say whether the iris belongs to the organs supplied by the sympathetic, or to those dependent on cerebro-spinal nerves. Its motions are involuntary, but, like the action of several feeble voluntary muscles, can be induced at will by being associated with the motions of parts under the influence of the third nerve (see page 684). We may perhaps explain in the same way the circumstance, that when the desire to pass the urine is very urgent, the action of the muscles in walking and running assists the effort to retain it, that is to say, tends to strengthen the action of the sphincter vesicæ. The heart itself, lastly, appears to have motor influence imparted to it in this way during strong muscular efforts of the body.

The remarkable phenomenon of the acceleration of the heart's action in voluntary muscular exertions has never been satisfactorily explained. It has been said that, under these circumstances, a larger quantity of arterial blood is required, and that on this account the heart must propel the blood more quickly through the lungs; but it does not follow that, because there is greater need of aeration of the blood, the motion of the heart should be modified in accordance with this end. The phenomenon has been accounted for, again, on the supposition that the passage of the blood through the heart and lungs is disturbed by the circulation being obstructed by the contractions of different muscles; the acceleration of the heart's action takes place, however, when the lower extremities merely are used, as in ascending mountains, running, &c. We cannot perceive how in the latter case the passage of the blood through the lungs and heart can be obstructed; for, though by the constant contractions of the muscles of the lower extremities the circulation is impeded in them, the blood which is not able to pass through the capillaries of these limbs will not reach the heart, and hence cannot accumulate there. The effect must be the same merely

* Hildebrandt's Anatomie, t. iii. p. 354.

as that of the application of a tourniquet to both thighs so as to impede the circulation in the lower extremities, by which nevertheless no acceleration of the heart's action is induced. It is possible, therefore, that this phenomenon, which is so remarkable in persons in a state of nervous debility, may be an associate action dependent on the communication of the nervous principle from the highly excited spinal cord to the sympathetic nerves. Since, however, this explanation cannot be regarded as strictly proved, and is merely supported by analogy with certain facts, it must at present be received merely as a suggestion for further inquiry.

The associate action of another organ endowed with the power of involuntary motion, namely of the vesicula seminalis, with voluntary movements, is much more evident. It has been remarked by many observers, that boys of irritable habit are liable, while using great muscular exertions, as in climbing, or in ascending a rope, to the occurrence of spontaneous excitement of the genital organs, and even to contraction of the seminal vesicles.

XX. *The motions of organs which derive their nerves from the sympathetic system, have a peristaltic type. The motions are progressive in a certain direction, and the course which the motions take is dependent not merely on the brain and spinal cord, but likewise on the nerves of the organs themselves.*—The cause of the peristaltic type is wholly unknown. The contractions of the intestinal canal succeeding each other like waves from above downwards, a second commencing before the first wave has traversed the whole intestine, are well known. The phenomenon is not confined to the intestine; the ductus choledochus also presents vermicular successive contractions, and even in the heart the motions are evidently successive. The movement of the heart in the incubated chick resembles a wave traversing the organ from behind forwards; in other words, it is peristaltic; and even in the heart of the adult the succession of the contractions indicates the peristaltic type. In the frog, the contractions of the muscular portion of the venous trunks, of the auricles, ventricles, and bulbus aortæ, succeed each other in the order in which the parts are here named.

The explanation of the regular succession of the motions in these organs is one of the most difficult problems in physiology, and has not hitherto been made the subject of any consideration.

It would, at first view, appear, that the cause of the succession of movements must be connected with the spinal cord itself. If, in the latter organ, waves or vibrations be supposed to succeed each other from above downwards, the fibres arising from the cord might successively receive the waves or vibrations, the result of which would be peristaltic motions of the intestine from before backwards. But this explanation is certainly unsatisfactory; for the successive motions of the

heart and intestines continue when these organs are removed from the body. The cause of these motions must therefore lie in the nerves themselves, which are ramified in the organs. The fibres of these nerves lie side by side; how can it happen that their action is successive? It might be attributed to an unknown spontaneous influence of the ganglia; but the motions still continue with the same type when the organs are entirely separated from the ganglia. In the present state of our knowledge, it is quite impossible to offer any probable explanation of the phenomena. We can merely indicate what kind of theory would be adequate in a mechanical point of view. A succession of motions determined by the nervous fibres might be imagined to take place, if the fibres running longitudinally along the intestine from before backwards gave off, at successive points, the nervous influence, or peripheral branches. In this case, currents slowly traversing the fibres might give rise to peristaltic motions of the intestine. A successive arrival of the nervous currents would likewise be attained, supposing that they were transmitted by a single nerve giving off, in succession, branches which increased in length in a certain direction, for example, from before backwards. We do not know that anything of this kind prevails in the distribution of the nerves in these organs; and the question is here referred to, only that the importance of the problem, the nature of a satisfactory explanation of it, and the impossibility of giving such an explanation, may be evident. What increases the difficulty of the question is, that in many cases the order of succession is alternately reversed, as in the phenomena observed by myself* in the leech, and by Mr. Lister† in the ascidia. In the stomach, too, the direction of the motions alternates in the normal state; and, in disease, the direction of the peristaltic motion both in the intestines and in the heart is sometimes reversed.

b. Of the sensitive functions of the sympathetic nerve.

I. *The sensations in parts, the nerves of which belong to the sympathetic system, are faint, indistinct, and undefined; distinct and defined sensations being excited in them only by violent causes of irritation.*—The facts illustrating this statement have been adduced at page 662. The faint and undefined character of the sensations may perhaps arise from the small number of sensitive fibres distributed to the parts supplied by the sympathetic nerve.

II. *The sensitive impressions received by the sympathetic nerve, although conveyed to the spinal cord, may not be perceived by the sensorium, the organ of consciousness.*—The action of a sensitive nerve continued to the spinal cord may give rise to sensation, or it may not; to produce a sensation it must be propagated with some degree of force to the brain; when it does

* Meckel's Archiv. 1828.

† Phil. Trans. 1834, p. 2.

not produce sensation, its influence is confined to the spinal cord, but it may give evidence of its affecting the cord by other signs than sensation, namely, by reflex motions (see page 709). Such motor actions of the spinal cord excited by impressions conveyed to it by sensitive nerves, which impressions do not give rise to sensations, are of frequent occurrence during life even in the healthy condition of the body, and they are the usual mode of action of the sympathetic nerve. It may be clearly shown that, in the production of these phenomena by the sympathetic nerve, the impression is really conveyed to the spinal cord, although it does not give rise to sensation. Any irritation in the rectum may excite a more active contraction of the sphincter ani; an irritation of the stomach, which is not productive of sensation, may nevertheless give rise to the action of the respiratory muscles which aid in vomiting. The motions of the respiratory muscles, which take place in vomiting, may be excited by an irritation, not productive of true sensation, in any one of the abdominal viscera, the intestinal canal, liver, kidneys, or uterus. Here the impression which commences the action, is made on the sympathetic nerve. The reflected motor influence affects cerebro-spinal nerves, not the sympathetic. It can be shown further, that the centripetal action of the sympathetic excites the motor power of the cerebro-spinal nerves through the intervention of the spinal cord, not of the nervous communications between the sympathetic and the other nerves: for although the sympathetic is connected with all the spinal nerves which act in producing vomiting, the connection consists merely in the fibres of the ramus communicans attaching themselves to the two roots of the spinal nerve,—there is no union of fibres; and since the motor root has no ganglion, we cannot, of course, explain the phenomena by supposing the influence of the sympathetic nerve conveyed by the ramus communicans to become diffused through the ganglion, so as to affect all the motor fibres which pass through it.

III. *The impressions which give rise to reflex motions, when conveyed to the spinal cord by the sympathetic nerve, are, in most instances, not productive of sensations; while those impressions which are received by cerebro-spinal nerves always give rise to sensations.*— This is true at least of the majority of cases. Irritation in the stomach, intestine, kidneys, uterus, or liver, which excites vomiting, does not affect the sensorium so as to produce real sensation. In all cases of reflex actions, on the contrary, excited through the medium of cerebro-spinal sensitive nerves, the exciting impression gives rise to a distinct sensation. Irritation of the mucous membrane of the larynx, trachea, or lungs, gives rise to a reflected action of the spinal nerves, so as to produce coughing; but a distinct sensation is induced by the irritation. The tickling of the fauces, which excites vomiting, is at the same time productive of a distinct sensation. Distinct sensation attends likewise the irritation of the nostrils,

which induces sneezing, and the action of light on the retina, which causes the contraction of the iris, or which, in other cases, causes sneezing.*

IV. *The ganglia of the sympathetic nerve do not prevent the transmission of centripetal actions in the sympathetic nerve to the spinal cord; they have not an insulating power over these centripetal currents.*—This results from the facts stated in the foregoing paragraphs; for since the irritation of the sympathetic nerve, which excites vomiting, is propagated to the spinal cord, although it does not give rise to true sensation, the ganglia cannot exert an insulating power over those centripetal actions. That such is the case, is, however, directly proved by an experiment which has been frequently mentioned, that of irritating the splanchnic nerve with a needle in a rabbit, the abdominal parietes of which had been completely divided, when, in many instances, a contraction of the abdominal muscles ensued at the moment of each application of the needle. The ganglia of the main cord of the sympathetic, from which the splanchnic nerve arises, cannot, therefore, have the power of arresting the transmission of impressions from the sympathetic nerve to the spinal cord: and the experiments of Volkmann on decapitated frogs prove the same fact with reference to the ganglia of the abdomen; for, by irritating the intestinal canal and other organs supplied by the sympathetic nerve, he gave rise to very extensive reflex movements of the trunk.

V. *The ganglia are likewise not the cause of the impressions on the sympathetic nerve being unattended with true sensation.*—This also results from facts already detailed. Brachet states, it is true, that but slight sensations, or none at all, can be excited in the thoracic ganglia of the sympathetic, and their cords of communication; while the rami communicantes between the ganglia and the spinal nerves are, he says, endued with distinct sensibility, and mechanical injury of them gives rise to distinct sensation of pain: a statement, however, which it is difficult to reconcile with the facts previously considered; for, in paragraph II, it was shown that irritation of the sympathetic nerve is propagated to the spinal cord, but gives rise to no sensation. Can it be, then, that the ganglia have the power of altering merely the quality or nature of the impression conveyed in the centripetal direction by the sympathetic nerve; that the impression is still propagated onwards, but deprived of the quality of pain? These questions become so abstract that it is impossible to answer them. The ganglia can have no influence on the actual perception of the impression by the sensorium. The circumstance of the impressions conveyed in the centripetal direction by the sympathetic nerve through the ganglia being unproductive of sensations, cannot be owing to any action of the ganglia themselves, since

* [The movements of the œsophagus in deglutition would appear, from Dr. Reid's experiments (see page 657), to be owing to a reflex action, excited through the medium of a cerebro-spinal nerve, though unattended with sensation.]

the perception of a sensation requires that the impression shall have been conveyed to the organ of consciousness. The cause, therefore, of the absence of sensations in the case of impressions made upon the sympathetic nerve, must be that these impressions are arrested in the spinal cord itself, and do not reach the seat of consciousness, where they would excite real sensation. Impressions on the cerebro-spinal nerves are always propagated to the sensorium in the brain; if in some cases they are not perceived, and produce no sensation, it must arise from the mind being directed to something else.*

VI. *In many cases, irritation of a violent nature in organs supplied by the sympathetic nerve, gives rise to sensations in those parts; in other cases, the sensations in the parts affected, the irritation being less violent, are indistinct, while distinct sensations are present in other parts supplied with cerebro-spinal nerves.*—We have examples of cases of the first kind in inflammations of the intestinal canal and liver; of those of the second kind, in the troublesome itching which is observed to affect the nose and anus in affections of the intestinal canal,—for example, when they are infested by worms; and at the glans penis in chronic diseases of the kidneys and bladder; while frequently no distinct sensations are perceived at the actual seat of the irritation. The pains which are sometimes felt in the upper extremities in diseases of the heart, and in the shoulder in diseases of the liver, are also examples of the latter kind of cases. They are instances of the radiation of sensations wholly analogous to the phenomena described at page 697 as the results of the radiation of sensations in cerebro-spinal nerves.

VII. *The secondary sensations in cerebro-spinal nerves, consequent on irritation of branches of the sympathetic, occur especially at the extreme parts of the organs affected.*—Thus we have itching of the nose from the irritation of worms in the intestinal canal, itching of the anus from irritation of worms in the large intestine, itching and pain in the glans penis from disease of the kidneys and urinary passages.

VIII. *That the ganglia exert a reflex action in the production of the sympathetic sensations is not proved, and many facts are opposed to the idea of their having such a function.*—Such are the experiments already detailed relative to the action of the spinal marrow in the production of the reflex phenomena; and, still more, several experiments related by Volkmann (see page 738, paragraph XIV.); and the result of these experiments renders it probable that the radiation of sensations likewise does not depend on the ganglia.

The secondary sensations in cerebro-spinal nerves have been commonly attributed to connections of the sympathetic with those nerves; and great influence has been ascribed to the ganglia of the sensitive roots of the spinal nerves, through which the primitive fibres of the roots

[* See note to former page.]

of the sympathetic as well as those of the cerebro-spinal nerves pass. This explanation appears still more improbable when we call to mind that the ganglia of the sensitive nerves cannot explain even the sympathetic sensations of the cerebro-spinal nerves themselves, since nerves frequently excite such sensations in each other which are in no way connected, and even are unprovided with a ganglion: thus, for example, the sympathetic tickling in the nose from the impression of the sun's rays on the retina cannot be explained by any connections of nerves; for although branches of the spheno-palatine ganglion of the sympathetic have been observed to join the ciliary or lenticular ganglion, and twigs of the sympathetic have been seen to accompany the vessels of the retina,—as, in fact, they do all vessels,—yet there is no well-established instance of a communication between the optic and nasal nerves. The affections of sight and hearing from diseases of the abdominal viscera likewise cannot be explained by such nervous communications, since they do not exist. Even supposing that the sympathetic nerve did send some twigs into the retina itself, that would not explain how an affection of the intestinal canal could act on the retina and alter vision; for, that such an effect should result, all the fibres of the optic nerve should pass through a ganglion. We know, however, that irritation of a single point of the retina does not extend beyond that point; the union of the sympathetic nerve with a single point of the retina could not possibly, therefore, excite a secondary sensation in it, except at that point, and could not produce a general change in the visual function. Hence, in endeavouring to explain the secondary sensations excited by primary affections of the sympathetic nerve, we meet with the same difficulties as we did in the case of the cerebro-spinal nerves; and it is more probable that all secondary sensations in cerebro-spinal nerves, excited by affections of the sympathetic, are produced through the intervention of the spinal cord and brain. It appears at first sight to be unfavourable to this view that frequently no sensation is felt at the seat of the irritation in the organs supplied by the sympathetic nerve, although the irritation excites sensation in a spinal nerve; but the centripetal action of the sympathetic nerve may be communicated to the spinal cord, without itself affecting the sensorium, and nevertheless give rise in the spinal cord to further actions,—for example, to real sensations in other nerves. That this is possible has been proved in paragraph II.

From the foregoing observations it may be gathered that the theory of the reflected sensations excited by impressions on the sympathetic is still very obscure, and, at all events, the mode of accounting for them is a subject of doubt.

c. Of the organic functions of the sympathetic nerve.

We are most unacquainted with the laws of the organic actions of the sympathetic nerve; for we have but just learnt that there are in all nerves, even in the cerebro-spinal, peculiar grey fasciculi, or organic fibres, on which depend the organic actions of the nerves in secretion and in nutrition. We have now to inquire whether in these nerves the motion or oscillation of the nervous principle can be propagated only in the centrifugal direction from the trunks and ganglia to the branches, or in the contrary direction; or whether the action of the nervous principle in these nerves can be exerted in all directions, a particular fibre of these nerves being capable both of transmitting a vivifying influence to a gland, and of exercising a reflex action so as to communicate the irritation in one gland to other organic nerves. It would be desirable also to know whether the organic nerves are, by virtue of their anastomoses, enabled to re-act on each other in such a manner that increased secretion from a whole surface may be excited by irritating one point, or whether all such reflex actions are effected through the medium of the spinal cord. The facts known relative to this subject admit of two explanations, and it cannot be determined with certainty which is the correct one. There are certain cases, however, in which either one or the other theory is more probable.

I. *When, in consequence of impressions on sensitive nerves, secretions take place in distant parts, the brain and spinal cord are probably the medium of communication.*—The irritation might here be communicated to the organic fibres by the ganglia of the roots of the sensitive nerves, which are traversed by fibres of the sympathetic; or it might be reflected upon the organic fibres by the spinal cord. The latter is evidently the most probable view, since the reflex action of the spinal cord in the reflected motions is a demonstrated fact, the reciprocal action of the different fibres in the ganglia of the sensitive nerves on each other a mere hypothesis. The cases of sympathetic affections of organic nerves here alluded to are very frequent. Impressions on internal mucous membranes,—for example, by drinks,—frequently give rise immediately to a general sweat. Violent impressions on sensitive nerves are sometimes followed by syncope, and with it a cold sweat. The latter phenomena are evidently the result of an influence reflected by the spinal cord, since the symptoms in syncope sometimes affect an extent of the system so great as to be explicable only by an action of the spinal cord. In some other cases of this kind it is more doubtful whether the phenomena may be explained in the same manner. Irritation of the conjunctiva of the eye and eyelids, attended with sensations, gives rise to a flow of tears; stimuli applied directly to the mucous membrane of the nose, or volatile stimulants affecting the same mucous membrane

when taken into the mouth, both producing violent sensations in the nose, likewise give rise to an effusion of tears. Mustard and horse-radish have this effect sometimes, even when taken into the mouth. It is usual to explain these phenomena by supposing the irritation to be communicated by the ethmoidal nerve to the trunk of the first division of the fifth nerve, and to be thence reflected upon the nervus lachrymalis: the secretion of tears from irritation of the conjunctiva has been explained in the same manner; the irritation of the conjunctiva being communicated to the first division of the fifth nerve, and thence again reflected upon the lachrymal branch. In both these cases, however, the explanation is defective; for, inasmuch as the fibres of a cerebro-spinal nerve are wholly distinct in their entire extent, an impression on one portion of its fibres cannot be reflected upon others. Others, again, have supposed the same phenomena to be the result of sympathy of the Schneiderian membrane with the lachrymal gland through the medium of the ganglion spheno-palatinum, which has been stated by some anatomists to be connected with the ciliary ganglion by means of sympathetic fibres. Now, since the ciliary or lenticular ganglion, by its long root, is connected with the nasal nerve, and thus with the trunk of the first division of the fifth, which gives off the lachrymal nerve, an immediate connection was thus found to exist between the spheno-palatine ganglion and lachrymal nerve. But the same objection must be made to this explanation as to the former; for, unless the fibres in the fifth nerve communicated with each other, an irritation conveyed through the ciliary ganglion and nasal nerve to the first division of the nervus trigeminus could not be reflected upon the lachrymal branch. There are still others who imagine the impression in the nose to be communicated to the Gasserian ganglion on the trunk of the fifth nerve, and to be thence reflected upon the first division of the nerve and its lachrymal branch. No objection could be made to this explanation of the phenomena, provided that we knew that the Gasserian ganglion, the ganglion of a sensitive nerve, were capable of giving rise to sympathy and reflex action; if it were proved that centrifugal nervous currents can take place in sensitive nerves, such as the lachrymal nerve; and if it were demonstrated that the lachrymal nerve really supplies the lachrymal gland with fibres which regulate its secretion. Since the secretion of tears, like other secretions, is determined probably by fibres of the sympathetic nerve, the most simple explanation would still be that which supposes the irritation to be conveyed from the nose backwards to the spheno-palatine ganglion, and, by means of the connection of all the organic nerves with each other, to be reflected in some way or other through the medium of organic fibres upon the lachrymal gland. But whether such a reflex action from sensitive nerves directly upon organic nerves, without the intervention of the brain and spinal cord, can occur, is the questionable point; and I know no other argument

in favour of its possibility than the impossibility of proving that it cannot occur. A very frequent instance of the reflex affection of the secreting function from irritation of a sensitive nerve is the increased flow of saliva often coming on quickly when food is taken into the mouth. The mode of the explaining the phenomenon is equally as uncertain here as in the former case. The assumption that the brain and spinal cord form the medium by which the irritation of the sensitive nerve is enabled to excite the organic action is at least favoured by the analogy of similar reflected actions of sensitive or motor nerves, through the intervention of the central organs.

II. *There prevails a consent of action between the different parts of a secreting membrane; thus, the state of one spot influences the condition of the whole extent of a mucous membrane. Here it is more simple to explain the phenomena by communication of the organic fibres with each other.*— Daily experience, in presenting us with general affections of mucous and serous membranes, shows the sympathy that exists between the different parts of a membrane, a sympathy which might be accounted for by the communication of organic fibres with each other; the explanation appears in this case more probable, nevertheless, its correctness cannot be directly proved.

III. *A particular state of one organ, such as inflammation or a secreting action in it, sometimes causes the production of a similar state in other parts. In this case we have an instance of reflected action of the organic fibres of one part upon those of another.*—Inflammation of the testicle may be replaced by inflammation of the parotid; erysipelatous inflammation of the skin may be transferred to the membranes of the brain; suppression of the secretion of one organ may give rise to increased secretion in another. All such phenomena are probably attended with changes in the organic fibres belonging to the sympathetic system, which accompany the blood-vessels. And here again the question arises whether such reflections are produced through the medium of the sympathetic alone, or whether the brain and spinal cord are the medium of reflection between the centripetal and centrifugal actions. There are no facts which enable us to decide this question; but in many cases it is probable that the sympathetic nerve alone is engaged in the production of the phenomena. In Mayer's experiments, ligature of the sympathetic nerve between the first and second cervical ganglia, was sometimes followed by an affection of parts which appear to be under the influence of the first cervical ganglion, namely, by inflammation of the eye. The peculiarity of the organic nerves, namely, the difficulty of distinguishing either origin or termination in them, their want of arrangement into trunks and branches, and the increase in their course which they frequently undergo, is certainly in favour of the possibility of their actions being propagated in all directions from the central points

of the ganglia, and not confined to centripetal and centrifugal currents. This view is also favoured by the circumstance, that, when an organ ceases to be supplied with organic fibres from one source, the supply may be furnished from another. Ligature of an arterial trunk without doubt injures the organic nerves which accompany it; nevertheless, no death of the part, atrophy, nor cessation of secretion in it, ensues; so that it appears as if the nerves accompanying the collateral vessels are able to supply the lost influence, or that the new supply is furnished by organic fibres in the spinal nerves. On the other hand, the influence of the spinal nerves may be lost without atrophy ensuing. In V. Pommer's experiments, too, it was observed that division of the sympathetic nerve on both sides of the neck gave rise to no injurious consequences, so that perhaps the influence of the divided portions of the nerve had been supplied from other sources, as, for instance, by the fibres accompanying the vertebral arteries. The metastasis of a morbid process, however, takes place in all cases towards the organ which is predisposed to it; thus, in persons with tendency to pulmonic affections, the metastasis takes place from the skin to the lungs; in patients liable to hepatic disease, from the skin to the liver; and in others, with irritable bowels, from the skin to the intestinal canal, and so on. In considering the laws of the balance which prevails among the secretions, not only the nervous system, but the nature of the different secretions, and their relation to the components of the blood and to one another, are to be attended to. The laws of the equilibrium of the secretions have, however, been already considered under the latter point of view, at page 473.

IV. *The ganglia appear to be the central parts from which the vegetative influence is distributed to the different organs.*—Inflammation of the eye, and even the general phenomena of impaired nutrition, have been observed to follow injury of the first cervical ganglion.

V. *This radiating influence of the ganglia appears to be in a certain degree independent of the brain and spinal cord,* since the embryo may be developed while the brain and spinal marrow are destroyed.*

VI. *It appears, however, that the brain and spinal cord are the main source whence the power of the organic nerves is gradually renovated, since certain affections of the brain and spinal cord, attended with paralysis, are likewise productive of atrophy.* (See the remarks on sleep at page 734.)—In concluding our inquiry respecting the sympathetic nerve, we can but lament the obscurity in which much regarding it is involved: still, we think to have shown how investigations on this subject must be prosecuted; and that, by applying the laws governing the action of cerebro-spinal nerves to the sympathetic, much light has been thrown on the properties of this nerve, of which M. Magendie seemed to think so little known that he hesitated to regard it as a nerve.

* See page 197 and Müller's Archiv. 1834, p. 268.

CHAPTER VI.

OF SYMPATHIES.

In the preceding chapters so many forms of sympathetic phenomena have been shown to depend on known laws of action of the cerebro-spinal nerves, independently of the sympathetic, that the latter nerve appears now to have little share in their production. The phenomena of the radiation and coincidence of sensations, of the associated and the reflected motions, are independent of the action of the sympathetic, and comprehend by far the greater part of the sympathetic phenomena formerly attributed to its influence.

We will now reconsider the sympathies under more general physiological points of view.

The sympathetic relations of the different parts of the system may be arranged under the following heads.

I. *Sympathies of the different parts of one tissue with each other.*

This is one of the most frequent kinds of sympathy. When different parts of a tissue suffer one by consent with the other, the secondary affection is ordinarily of the same kind as the original one.

a. Cellular tissue.—There is a great tendency in the cellular tissue to the extension of any particular state from one part through all its prolongations. The diseases of the cellular tissue,—emphysema, œdema, induration, fatty degeneration, inflammation, and suppuration,—afford examples of this tendency. They often spread over large tracts between the muscles, vessels, and aponeuroses, following merely the connections of the interstitial cellular tissue. Hence it is that a knowledge of the natural boundaries of the cellular membrane, namely, the fasciæ, is so important in forming our judgment of suppurations in it.

b. Skin.—Although there is a marked sympathy between the skin and internal organs, yet between the different parts of the skin itself there does not appear to exist any great reciprocal influence. Simple inflammation of the skin may be confined to one part. But the skin may become the seat of extensive exanthematous inflammation, acute as well as chronic, from its having, by virtue of its office of a secreting organ, a certain affinity for morbid matters circulating in the fluids of the body. It sympathizes much more frequently, however, with internal parts, for which it forms the common exterior envelope. Instances of such sympathies will be given hereafter.

c. Mucous membranes.—In the mucous membranes there is, it is well known, a great tendency to the communication of a particular state of one tract to others with which it is continuous, as, for instance, in catarrh.

d. Serous membranes.—A primary affection of one serous membrane is often followed by a similar affection of all the others. Thus to ascites is added hydrothorax ; all cases of dropsy affecting different parts are not, however, examples of sympathy. Dropsy frequently arises from the introduction of morbid matter into the blood in several parts simultaneously, or even from obstruction to the circulation in one important organ. In these cases, therefore, the simultaneous affection of the different serous membranes is owing, not so much to sympathy of the membranes themselves, as to the circumstance of the original cause having an extensive sphere of action.

It is really owing to sympathy, however, when, in consequence of inflammation of one serous membrane, others become inflamed. Thus, sometimes inflammation of the peritoneum is followed by pleuritis and arachnitis; the latter, from being seated in the most important organ, is perhaps the cause of death.

e. Fibrous membranes.—There is such a close sympathetic connection between the fibrous membranes, that a local lesion very frequently induces an extensive and violent affection of them. A local rheumatic affection is very prone to extend to all the fibrous tissues connected with its original seat, and change its locality; always following, however, with most facility, the connections of the fibrous membranes. Injury of the ligaments, aponeuroses, and fibrous ligamentous tissues of the foot or hand, frequently gives rise to extensive inflammation, swelling, and pain, which spread from the first point of irritation over the sheaths of the muscles, and sometimes attack even the periosteum.

It may be inferred that the nerves have a share in the sympathies of the fibrous membranes, partly from the presence of organic nerves accompanying the vessels in all vascular tissues, and partly from the actual existence of nerves in the dura mater. Nerves have been seen in the dura mater by Comparetti, Arnold, Schlemm, Bidder, and myself: they are in part referable to the system of organic fibres.

f. Bone and cartilage.—Instances of sympathy in the osseous system are rare. In many diseases, as in rhachitis and secondary syphilis, the osseous tissue throughout the body is affected, but these structural diseases can scarcely be arranged among the sympathies; there is here general irritation, with morbid formation of the osseous matter. There are, however, also distinct examples of sympathy in the bony tissue. Thus, when an irritating influence acts upon the surface of a cylindrical bone, the inflammation which ensues is seldom confined to the surface, but affects the whole thickness of the bone, even to the medullary membrane; the texture of the bone becomes changed in its whole thickness: so likewise when the medullary membrane of a bone is destroyed, the bone becomes inflamed and swelled internally, and also externally, to its very surface. We are at present unacquainted with

the nerves of the bones, but must pre-suppose the existence of organic nerves accompanying the vessels in them, as in all vascular parts.

g. Muscle.—Muscle has been supposed to enjoy, in a high degree, the property of being excited by sympathy. In proof, it has been stated that the irritation which causes the contraction of one muscle, is frequently attended with a number of sympathetic actions of other muscles; but here the sympathy is not a property of the tissue itself, but of the motor nerves: a muscle of which the nerve is cut off from the rest of the nervous system is, it is true, still irritable, contracting under the influence of an external stimulus; but the irritation is never communicated to other parts of the same tissue,—no sympathetic muscular motions ensue.

The sympathetic convulsions of the muscular system are, therefore, not properly sympathies of the muscular tissue, but nervous sympathies. The remaining small number of morbid actions which occur in muscles, as inflammation and suppuration, are always limited in extent, and do not spread beyond the original seat of the irritation, as they do in other tissues. In addition to the very rare inflammatory affection of muscle, its degenerations, and the spasmodic affections, scarcely any other disease is known to attack this tissue. It is evident, from a consideration of all these facts, that in the muscular tissue no very great sympathy prevails, either between its different parts, or between it and other tissues.

h. The lymphatic system comprehends the lymphatic vessels and glands.

Diseases of the lymphatic system are very rarely local; when originally seated in this system, and not sympathetic of diseases of other organs, they usually affect it generally, constituting a morbid diathesis; some diseases, as scrofula, indeed, seem to be confined nearly entirely to the lymphatic system. If the irritation be at first local, it rapidly spreads by sympathy. When a lymphatic gland becomes inflamed in consequence of external irritation, the surrounding glands soon become affected; they become swollen, if not actually inflamed. Many primary irritations of the lymphatic system are produced by irritating substances (poisons) absorbed into the lymphatics. The inunction of mercury at one part of the surface often gives rise to extensive irritation of the lymphatics, and the glands of different parts of the body become simultaneously affected. Inflammation of the lymphatics from the local action of a poisonous substance rapidly extends to all the lymphatics in the limb; and in such cases the skin is everywhere traversed by red lines, indicating the course of the inflamed vessels.

Of equally frequent occurrence are instances of the sympathy of the lymphatic vessels with lymphatic glands. One of the most common symptoms in structural diseases of the great viscera is enlargement of the lymphatic glands in the neighbourhood.

Sympathetic enlargement of the lymphatic glands is equally frequent in inflammatory affections of a neighbouring part.

These sympathetic enlargements of the glands differ chiefly from the original affection in disappearing as soon as the disease of the organ primarily affected is removed; in being chronic when excited by a chronic disease, acute when the primary disease is acute; and, lastly, in consisting simply of tumefaction, generally without any other change from the natural state of the tissue.

We may state generally that an extensive irritation of the lymphatic system may be excited from any point of the surface which is supplied with lymphatic vessels. The exciting cause may either be the actual introduction of an irritating matter, or a lesion unattended by absorption; for example, a mechanical injury, or a burn. Hence, we see that for the excitement of this sympathy it is, at least, not indispensable that a morbid matter be actually carried along the vessels. The irritation of the lymphatics may be excited, too, by original irritation of an internal surface of the body, just as, by lesion of the external surface, when a corresponding series of phenomena ensues. Just as inflammation of the skin from a burn is followed by irritation of the surrounding lymphatics, extending to the nearest lymphatic glands, so inflammation of the mucous membrane of the intestinal canal, when it continues for any length of time, induces inflammation of the lacteals and mesenteric glands,—those lacteals and glands, namely, which correspond to the inflamed part of the intestine; of this we have a distinct example in the ulcerations of the intestines in typhus.

Sometimes the lymphatics as well as the veins, coming from a suppurating part, contain pus. The corresponding lymphatic glands also occasionally suppurate. It would be an error to infer that the pus in these cases had been absorbed by the lymphatics; it is produced in the vessels themselves by the inflammation which has extended into them, just as the pus in the veins of the stump of an amputated limb is produced by inflammation of their coats. The inflammation and suppuration of the mesenteric glands, consequent on ulceration of the intestines in typhus, afford us a distinct proof that in this case, at least, the pus is formed in the absorbent vessels and glands themselves.

i. Blood-vessels.—When it is remembered that the sympathy of the pulse with the diseases of individual organs depends on a sympathy of the heart, rather than of the arteries themselves; and when, moreover, it is taken into consideration that the local diseases of arteries, such as inflammation and dilatation, are in a great measure limited to the point to which their exciting cause was applied, and have no tendency to spread; we are justified in the conclusion that the sympathies of arteries are in general inconsiderable: we must, at least, adopt this opinion with regard to the coats of the larger arteries and their branches.

But we cannot doubt that the nervous system may exert an influence over the state of the arteries independently of the heart; this influence is seen in the varying state of turgescence of the skin during mental emotions, the local congestions and succeeding collapse which are observed to occur in different parts of the surface from mere mental emotions.

In cases of a general affection of veins, it is difficult to determine whether this has originated at one point, and gradually spread from sympathy of tissue, or whether the immediate cause of the disease has acted simultaneously on a great extent of the venous system. It is, however, a character of this system of vessels, that its diseases are generally not local.

We have direct proof of the extended sympathy of the veins in phlebitis, which being excited at any point, by causes capable of giving rise to inflammation, extends so rapidly, that in a short space of time all the venous trunks of the limb become affected.

k. Glandular tissues.—Although certain diseases, as scrofula and cancer, attack principally the glandular tissue, yet these general affections of the glands cannot be attributed to sympathy, but arise from the nature of the diseases themselves, which have an especial tendency to affect glandular structures; and their extension is not so much the consequence of an original local irritation, propagated by sympathy, as of a general morbid disposition of the tissue developed to a complete disease under the influence of local irritation. There is no doubt, however, that when a disease commences in a single gland, it will, from the sympathy of the different parts of the gland, more readily affect the whole of its substance than other surrounding textures. The following are instances, however, of sympathetic irritation of glands.

All secreting organs, just as they reflect irritation in themselves upon their efferent ducts, are also sympathetically affected with irritation when their efferent ducts are first affected; thus the presence of food in the mouth gives rise to an increased flow of saliva from the salivary glands, the presence of a sound in the bladder excites an increased secretion of urine (?), irritation of the glans penis an increased secretion of semen, irritation of the mucous membrane of the eye a more abundant secretion of tears. Thus also, while the food is in the stomach, the bile flows into the small intestine in small quantity; but, when the chyme has come into contact with the mucous coat of the duodenum, it is poured out in much greater abundance; during fasting, on the contrary, the amount of bile excreted is very scanty.*

* The facts considered in this section have been elucidated by the principles of physiological anatomy, chiefly through the labours of Bichat, whose work on general anatomy contains more of the true principles of general pathology than most of our treatises on that subject.

It is difficult to account for the sympathy evinced by different parts of a tissue for each other. It has been supposed to be independent of nervous action, and to be owing to the uniformity and continuous course of the tissue. But can inflammation, for example, really spread in a tissue by this kind of contagion? Can the component substance of a tissue, independently of nervous influence, by a kind of affinity of its different parts communicate a state of irritation from one point to those contiguous? We cannot decide this question. Other physiologists have attributed these sympathies of a single tissue to the influence of the nerves, inasmuch as mucous membranes which are not anatomically connected, and serous membranes which do not communicate in any way, present phenomena of sympathetic consent. But still another explanation of such cases might be offered, namely, that all the phenomena are owing to a noxious matter absorbed into the blood or generated in it, which has an affinity for all mucous or all serous membranes, &c. The nerves are, however, evidently engaged in the cases of the extension of sensations over the different parts of a tissue; but whether by virtue of a connection of their peripheral extremities, or through the intervention of the central organs of the nervous system, is another question.

II. *Sympathies of different tissues with each other.*

This second form of sympathy is of much less frequent occurrence than the first. Ordinarily a disease has a much greater tendency to affect the same tissue in a different organ from that first affected, than to be communicated from one tissue to another even in one and the same organ. The mucous coat may take on a morbid secreting action, without the muscular coat suffering; the serous covering of the heart may be the seat of disease, while the muscular substance under it remains healthy; the muscular coat of the intestinal canal may be affected with spasm, the mucous and serous coats remaining in their normal state. The serous tunic of an organ may secrete a watery fluid without the other tunics being affected. There are instances, however, of sympathy between different tissues. It is here to be observed, that when different tissues sympathize with each other, the phenomena vary in them according to the properties of each; while in the sympathy of different parts of the same tissue, the secondary affection is ordinarily identical in its nature with the original one; inflammation alone manifests itself with the same characters even when it affects different textures. The principal examples of this second form of sympathy are the following:

1. *Between the skin and mucous membranes.*—These textures very frequently sympathize. Many diseases of the mucous membranes, particularly inflammation and increased secretion, are frequently excited by the action of a noxious influence on the skin, and *vice versâ*. The

action of cold upon the skin gives rise to inflammation of the lungs, throat, or intestines, or catarrhal affections of these or other mucous membranes; the mucous membrane of that organ being always attacked, which, from idiosyncrasy of the individual, is more disposed to disease than the skin. On the other hand, a diseased state of the mucous membranes, for example, of that of the stomach, induces an altered condition of the secretion of the skin, of the circulation in it, and of its colour. Owing to the sympathy of the mucous membranes with the skin, we can arrest hemorrhages from the former by the application of cold to the latter structure.

2. *Between the skin and serous membranes.*—The effusion of a watery fluid from the serous membranes is always attended with diminished secretion from the skin; and suppression of the cutaneous secretion sometimes gives rise, on the other hand, to effusions into the serous cavities, as well when the skin is in a healthy state, as when it is the seat of an exanthematous eruption the course of which is disturbed. Lastly, inflammations of the serous membranes are not infrequently excited by the action of noxious influences upon the skin.

3. *Between the glandular tissue and the mucous membranes.*—I have already mentioned how close a sympathy prevails between the mucous membranes, and the glands which pour their secretion into them. At this we must not be surprised; since the glandular tissue is not merely a developement, as it were, of the efferent duct, and this a prolongation of the mucous membrane, but the glands connected with the intestinal canal are originally formed as diverticula from it.

4. *Between the mucous membranes and the serous membranes*, such reaction is of more rare occurrence.

5. *Between the fibrous membranes, as the periosteum, and the cartilaginous and osseous tissues*, there is a very close sympathy. The state of the periosteum determines that of the bone, and *vice versâ*. Inflammation of the periosteum is frequently followed by enlargement of the bone beneath it; and, when swellings of the osseous substance itself take place, the periosteum becomes thickened. Enlargement of the whole thickness of a bone is a result of inflammation of its medullary membrane. Destruction of the periosteum gives rise to external, destruction of the medullary membrane to internal, necrosis. This relation depends principally on the circumstance that innumerable minute vessels are received by the bone both from the periosteum and the medullary membrane.

An observer of the phenomena of disease will easily multiply the examples of sympathy between different tissues. The same explanation is not applicable to all such cases. Secreting membranes by virtue of their influence on the circulating fluids, and independently of the nerves, stand in an antagonistic relation to each other. Other phe-

nomena, in which it is not so much the secretion only, as the whole vital condition of the membranes, which is altered, as in the reaction of the skin and mucous membranes on each other, are rather to be referred to the effects of reflex action of the nerves. With respect to the sympathy of the glands and mucous membranes, it is uncertain whether it be owing to reflection, or to the direct action of the nerves on each other, by the intervention of the sympathetic. The sympathy of the periosteum and medullary membrane with the osseous substance is to be ascribed to the vascular communication, and to the sympathy of the vascular tissue common to them.

III. *Sympathies of individual tissues with entire organs.*

A disease of an entire organ, into the formation of which a tissue that extends to other parts enters, affects also the prolongations of this tissue; and, on the other hand, the state of a single tissue may modify all the others, which with it form a compound organ. Examples of this kind of sympathy may be found more particularly in the relation existing between the viscera and the skin, and the mucous and serous membranes.

Through the medium of the skin noxious influences may set up disease in any internal organ predisposed to it; and, on the other hand, the application of irritants and derivatives to the skin has an effect on a diseased state of any organ lying near the part irritated. Hemorrhages from internal parts are arrested by the action of cold upon the skin. Lastly, an exanthematous disease may disappear from the skin, and affect an internal organ.

The serous membranes always participate in the condition of the organs to which they give an investment. When the viscera are the seat of structural disease, the serous membranes take on a morbid action, not merely where they cover the diseased organ, but in their whole extent. Thus, organic disease of the lungs gives rise to hydrothorax, of the heart to hydro-pericardium, of the uterus and ovaries to ascites, and of the testis to hydrocele. When viscera, of which mucous membranes form part, are diseased, those membranes are always affected in a great extent. Organic diseases of the uterus are attended with leucorrhea; diseases of the lungs, with affection of the bronchi; and structural diseases of the stomach and intestinal canal, frequently with obstinate constipation from defective secretion of the intestinal mucous membrane.

The whole system sympathises with the inflammatory state of a mucous membrane; and the surrounding muscles either act with difficulty, as is the case with the pharyngeal muscles in inflammation of the pharynx; or they are affected with spasms, as when irritation of the lungs gives rise to spasmodic action of the diaphragm and intercostal muscles, so as to produce coughing. Mechanical irritation of the mucous membranes

has the same effect. Every one has observed the convulsive actions excited by mechanical irritation of the glottis, the retching from irritation of the mucous membrane of the pharynx: irritation of the mucous membrane of the bladder or ureters by calculi, or inflammation, gives rise to spasmodic contraction of the sphincter ani, of the sphincter vesicæ, and to drawing up of the testicle by the cremaster. For the explanation of these latter phenomena we refer to page 714.

Of all membranes the fibrous have the least sympathy with other organs, even with the organs which they invest. These fibrous membranes, which have the office of affording protection or attachment to other parts, are in this respect almost insulators. Inflammation only of these membranes can affect the organs which they invest, and give rise to marked symptoms in them, and this depends on the communication and sympathy of their vessels; hence it is that inflammation of the dura mater is attended with cerebral symptoms.

The explanation of the sympathy of individual tissues with entire organs is to be found partly in the laws of nervous reflection, when the sympathizing parts are quite unconnected, and partly in the reaction of communicating vessels, and of the nerves accompanying these vessels in parts which are connected, such as the uterus and the mucous membrane of the genital organs.

IV. *Sympathies of entire organs with each other.*

Although it is essential to our ideas of a living organism that the condition of one organ has an influence on that of all the others, yet this influence is manifested principally between organs of certain systems or groups. The sympathies which fall under this head are the following:

1. Between organs which have similar structure and function; as between the different salivary glands, between the heart and blood-vessels, between the stomach and intestines, and between the different central organs of the nervous system.

2. Between organs which, although of different structure, yet belong to the same system; such as the different organs of the chylopoetic system (intestinal canal, glands, and spleen), the uropoetic system, the generative system,—the two latter systems reacting on each other,—and the respiratory system of organs (larynx, trachea, and lungs).

3. Between organs which are anatomically connected by means of vessels and nerves, as the lungs and heart.

4. Between all important viscera and the central organs of the nervous system. We have instances of such sympathy in the affection of the brain which accompanies inflammation of the viscera, as of the liver, lungs, or intestinal canal; and in the affections of the stomach and liver, which attend injuries or irritation of the brain, &c.

The phenomena of this class are partly owing to the different organs of the same system, or parts anatomically connected, deriving their nervous influence from one and the same source; partly to the influence of the central organs of the nervous system upon all the organs of the body. The probability of these phenomena being in a greater degree dependent on the central organs than on the anastomoses of the sympathetic nerves, is evinced by sympathies which are quite inexplicable by nervous communication or anatomical connection; namely, by the sympathies between the mammæ and genital organs, of the larynx and respiratory organs with the genital organs at the period of puberty, and in debauchees and eunuchs. The sympathy of the parotis and testicle in the metastasis of inflammation from the one to the other, is at present inexplicable, except on the principle of reflection.

V. *Sympathies of the nerves themselves.*

Although the nerves are the cause of the greatest part, if not of all, of the phenomena of sympathy, yet we must consider separately those cases in which the reciprocal action takes place between nerves only, or in which the secondary phenomena at least are manifested by a nerve.

I. *Sympathies of nerves with the central parts of the nervous system.*—Not only do the nerves require, for the preservation of their natural power, the influence of the central organs to be constantly transmitted to them; but a change can be produced in the central organs through the medium of the nerves. The facts showing this have been already in part detailed in the chapter on nervous reflection (p. 711). We avail ourselves of this sympathy of the central organs with the nerves in a number of cases of disease of the brain and spinal cord. The spinal cord itself may be stimulated through the nerves which arise from it, by friction of the skin and other means. The brain and spinal cord also may be excited through the medium of the nerves by cold and warm baths, shower-baths, and the dropping of cold water upon different parts of the surface. These facts have been long known, but not the physiological laws by which they may be explained; the facts detailed in the chapter on nervous reflection enable us to understand how the nerves and central organs can sympathise with each other. The application of mechanical, galvanic, or chemical stimuli to the nerves, in any part of the body, particularly in the skin, gives rise to powerful centripetal action; which, if often repeated, is calculated to rouse the depressed vital process in those parts of the brain and spinal cord from which the stimulated nerves arise, and indirectly in other parts of the central organs of the nervous system. We may, from these considerations, deduce the inference that, in the treatment of diseases, the central organs may be acted on in very different ways, namely:

1. Directly, by means of matters introduced through the medium of

the alimentary canal, or of the skin, into the blood; a method which is often unsuccessful, on account of the insufficiency of the remedies.

2. By acting upon the nerves arising from the central organs; a procedure which is attended with the most excellent results.

II. *Sympathies of the sensitive and motor nerves with each other.*—In the foregoing case we have regarded merely the effects which impressions made upon the sensitive nerves induce in the central organs themselves; here we have to consider reactions of the central organs thus stimulated upon other sensitive or upon motor nerves. The centripetal excitement of the sensitive nerves does not merely act upon the central organs, but is reflected from them. This reflection sometimes takes place from one sensitive nerve upon another. Hence we are enabled to stimulate sensitive nerves, which are not directly accessible to us, such as the auditory or optic nerves, by applying the stimulating means to other sensitive nerves which stand in relation with them, both physiologically and in respect of origin. Thus, we treat partial deafness and imperfect loss of vision by irritants to the skin, &c. By virtue of the reflected action of sensitive upon motor nerves, with the intervention of the brain and spinal cord, we are sometimes enabled to remove local paralysis of individual nerves, for example, of the facial nerve, in ptosis, by irritating the nerves of the face, &c.

III. *Sympathies of the corresponding nerves of the two sides.*—Of this we have instances, particularly in the optic, auditory, and olfactory nerves, and in the ciliary nerves.

When one eye is affected with a disease, and originally but this one, the other is frequently attacked by the same disease. One eye being destroyed by inflammation, the other frequently becomes inflamed and also disorganised. Affections of the internal ears are not always confined to one side. Deafness of one is often followed by the other becoming deaf also. The sympathies of the motor nerves of the eye, and especially of the ciliary nerves, are sufficiently well known. In the healthy state the sympathy of the nerves of the two irides causes the pupil to be of equal size, although the external influences are most different on the two sides. The sympathy of the corresponding nerves of the opposite sides is evidenced very frequently in what are called neuralgic diseases,—the painful affections of the nerves. In consequence of painful affection of the nerve on one side of the face, the corresponding nerve of the other side sometimes becomes affected. Toothache from a decayed tooth is not confined to the seat of the irritating cause: the corresponding nerve of the opposite side is occasionally affected.

IV. *Sympathies of motor nerves with each other.*—The extremely frequent phenomena of associate motions, the movements which involuntarily accompany other movements determined by the will, have been treated of at page 683.

V. *Sympathies of sensitive nerves.*—These present themselves principally under three forms, which differ merely in the extent and distance from each other of the parts thrown into consensual action.

a. In the first case a violent sensation excited at a single spot extends to nerves of the same kind, or to other fibres of the same nerve; a phenomenon which has been treated of under the head of the "radiation of sensations," at page 697.

b. In the second case, an affection of one sensitive nerve induces an affection of a sensitive nerve of another kind, but in the same organ. This kind of sympathy is observed principally between the nerves of special sense and the nerves superadded to the organs of sense, for the reception of the general impressions of resistance, warmth, cold, pleasure, and pain. The optic nerve is susceptible of the impression of light; but, according to M. Magendie, is not endued with common sensation: the eye receives common sensibility from branches of the fifth, which ramify in the conjunctiva, and from the ciliary nerves. The organ of hearing has, in addition to the auditory nerve, fibres from the facial, the second, and third division of the fifth nerve, and from the ganglion oticum, which are distributed in the mucous membrane of the tympanum; and from these, together with the numerous nerves of the external ear and external meatus, the common sensibility of the organ of hearing is evidently derived. The nose is not only the seat of the sense of smell, derived from the olfactory nerves, which, according to Magendie, are devoid of common sensibility, but is very susceptible of other sensations, such as resistance, warmth, cold, tickling, pain, &c. which depend on the nasal branches of the fifth nerve. The tongue has the sense of taste, but also the sense of touch, as every one knows.

Now, the nerves of special and those of common sensation in the organs of sense have a marked influence on each other. The blindness which sometimes follows injury of the frontal nerve has been thought to be an instance of this. It has been imagined that the effect of the injury of the frontal nerve is propagated backwards to the trunk of the ophthalmic, from the nasal branch of which the ciliary ganglion derives its longer root. But the ciliary nerves can influence the power of the iris only, not that of the retina, with which they are in no way connected. It appears to me much more natural to suppose that the consecutive blindness after contusions of the forehead is owing to the concussion suffered by the eye and optic nerve. M. von Walther has, I think, gone too far in attributing much influence to the ciliary nerves in the production of amaurosis and amblyopia. In many other phenomena, however, we have indubitable proofs of the sympathy of the different nerves of the organs of sense; for example, in the sensation of tickling in the nose from looking at the sun, and in the sensation of shuddering, and creeping over the surface, excited by certain sounds, &c. The principles laid down in the section on the

laws of nervous action do not leave much doubt concerning the explanation of these phenomena. Since communications of the nerves of special sense with the superadded nerves of common sensation, by means of the sympathetic, have not been satisfactorily demonstrated to exist, we must refer the phenomena in question to reflection of the impression in the brain. Tiedemann,* in treating of the sympathies of the organs of the senses, lays stress upon the fact that all those organs receive branches from the sympathetic nerve; this cannot be denied; but, to explain the sympathies of the nerves of special sense with other sensitive nerves, it is necessary, not that the organ generally, which is a part composed of numerous tissues, but that the nerve itself should have such connections with the sympathetic. Such connections have indeed been described. Tiedemann himself saw branches of the ciliary nerves accompanying the arteria centralis retinæ, even as far as the retina; but this does not prove a connection of the optic nerve or of the retina with the sympathetic. Hirzel † observed in several cases a connection between the ganglion spheno-palatinum and the optic nerve. Arnold traced such a twig as far as the sheath of the optic nerve, and denies its connection with the nerve itself. Varrentrapp ‡ did not see this communicating filament. But even if the optic nerve did really receive a filament from the sympathetic, much would not thereby be explained; for, to establish such a communication as is necessary to explain the sympathies, the communicating thread of the sympathetic must be connected with all the fibres of the optic nerve; its connection with one or a few of these fibres would not be sufficient. The same remarks apply to the organ of hearing. Koellner, Swan, Arnold, and Varrentrapp have observed a connection between the facial and the acoustic nerve, within the meatus auditorius internus. According to Arnold, § the communication is two-fold; one is through the medium of the sympathetic nerve. A fibre derived from the sympathetic leaves the facial to join the acoustic nerve, and in the calf forms a small ganglion at the bottom of the meatus auditorius. This structure, which is very distinct in the calf, appears to me to be destined to convey organic fibres into the interior of the labyrinth. The organic fibres also of the tympanic plexus may probably be subservient to the organic functions, such as the secretion of mucus. The second mode in which the facial and acoustic nerves are connected, is by means of a fibre which passes from the smaller portion of the facial nerve to the nervus acousticus. Since at their origin the two nerves are connected by many nervous filaments, this communicating thread in the meatus auditorius may be regarded as a fibre which belongs to the acoustic nerve, but

* Zeitschrift für Physiol. i. 237.

† Tiedemann's Zeitschrift, i. 229.

‡ Observ. Anat. de parte cephal. nerv. sympath. Francof. 1831.

§ Der Kopftheil des veget. Nervensyst. Heidelb. 1831; p. 83.

which has thus far accompanied the facial. The ramus acusticus accessorius, derived from the facial in birds and the cyclostomatous fishes, is to be viewed in the same light.

The remarks which we have made regarding the sympathies of the nerves of special sense with the other superadded nerves of the organs of sense, may be applied to the more remote sympathies of these organs with the abdominal viscera. Partial amaurosis, tinnitus aurium, and other symptoms, have been observed accompanying a disturbed state of the functions of the abdominal viscera; and many persons have explained these phenomena on the supposition of the sympathetic nerve having a share in the functions of the organs of sense, although they are much more easily accounted for as the result of the impression made by the disordered viscera upon the brain and spinal cord, and by them reflected upon the organs of sense. These secondary affections of the senses cannot, however, be regarded in this isolated manner; the whole nervous system frequently suffers in such cases; obstinate pains in the head precede or accompany the affection of the organs of sense, or the sensibility of the nerves of common sensation generally is found to have suffered. Having now considered separately the different forms of sympathy, we must glance at its application to the treatment of disease.

The principle of the balance of sympathy teaches us how we must avoid aggravating the morbid condition of one organ by the means which we apply to another; but it also teaches us how we may produce a change in the state of one organ directly inaccessible to us by effecting an appropriate change in another. The remedial means which act by virtue of the sympathies of the body have received the names of derivation and counter-irritation, inasmuch as they are intended to remove a certain state in one organ by inducing artificially a change in another. Their mode of action may be thus stated:

1. By increasing the activity of an affected part, by artificially increasing that of the part which sympathises with it.

2. By lessening the irritation of a part, by producing relaxation of the consensual part.

This result may be expected in the highest degree in the sympathies of the nerves, and especially wherever the laws of reflection from sensitive upon motor nerves, by the intervention of the brain and spinal cord, come into play. In the nerves distributed over the whole surface of the skin, we have an extensive field for acting indirectly on the brain and spinal cord. By friction, electricity, moxas, cold baths, and mustard plaisters, we stimulate the peripheral extremities of the cutaneous nerves, and indirectly the central organs of the nervous system; by soothing the peripheral nerves in the skin by tepid baths, we allay irritation of the brain and spinal cord.

3. Diminution of a morbid secretion in one part, A, by increasing the

secretion of another part, B, or by giving rise to a similar secretion in the second part, B. This mode of action is the reverse of that which takes place in the preceding cases; it is explained by the principle of the antagonism of secretions, laid down at page 473. There is an exception to this law in the sympathy of the different parts of one and the same tissue (see page 751).

4. Diminution of sanguineous congestion in one organ, by exciting congestion artificially in another organ; as in the action of hot foot-baths. This case is similar to the preceding, and is the reverse of the first two, but is explicable on the same principle.

5. Diminution of a certain state, x, in one part, A, by exciting a different state, y, in a second part, B, of the same tissue; a method which we adopt frequently with the best effects. Secretion and inflammation, particularly when seated in a secreting organ, are to be regarded almost as opposite states. Inflammation always arrests the natural secretions. Hence inflammation of the mucous membranes of the fauces is successfully treated by exciting a diarrhœa. The same reaction can be excited between different tissues. A diarrhœa diminishes congestion in the head. This case, however, belongs to the mode of action indicated at paragraph 4.

6. Diminution of a certain state, x, in one organ, by exciting the same state in another organ. This appears to be contradictory to most of the facts established in the foregoing paragraphs, and its explanation is a matter of great difficulty. The production of an inflammatory state artificially in the neighbourhood of an inflamed part would cause the original inflammation to become increased, not diminished, particularly if the artificial inflammation was induced in a part of the same tissue; and, nevertheless, inflammation of one organ is rendered less active by inflammation being excited in another organ, at a certain distance from the organ originally diseased. Inflammatory affections of the eye are treated by exciting inflammation of the skin at a little distance from the eye. Affections of the joints, &c. are treated by counter-irritation of the skin. The success of these methods of treatment seems to prove, that the states of irritation of the capillary vessels of two organs, particularly if in different tissues, are not subject to the same relation which we have observed to prevail so distinctly, in the cases indicated in paragraphs 1 and 2, between peripheral and central parts; and by virtue of which, irritation of the peripheral branches of the nerves does not arrest irritation of the central organs, but induces in them a more active state.

SECTION IV.

Of the peculiar properties of individual nerves.

CHAPTER I.

OF THE NERVES OF SPECIAL SENSE.

The nerves have always been regarded as conductors, through the medium of which we are made conscious of external impressions. Thus the nerves of the senses have been looked upon as mere passive conductors, through which the impressions made by the properties of bodies were supposed to be transmitted unchanged to the sensorium. More recently, physiologists have begun to analyse these opinions. If the nerves are mere passive conductors of the impressions of light, sonorous vibrations, and odours, how does it happen that the nerve which perceives odours is sensible to this kind of impressions only, and to no others, while by another nerve odours are not perceived; that the nerve which is sensible to the matter of light, or the luminous oscillations, is insensible to the vibrations of sonorous bodies; that the auditory nerve is not sensible to light, nor the nerve of taste to odours; while, to the common sensitive nerve, the vibrations of bodies give the sensation, not of sound, but merely of tremours? These considerations have induced physiologists to ascribe to the individual nerves of the senses a special sensibility to certain impressions, by which they are supposed to be rendered conductors of certain qualities of bodies, and not of others.

This last theory, of which ten or twenty years since no one doubted the correctness, on being subjected to a comparison with facts, was found unsatisfactory. For the same stimulus as electricity, may act simultaneously on all the organs of sense,—all are sensible to its action; but the nerve of each sense is affected in a different way, becomes the seat of a different sensation: in one, the sensation of light is produced; in another, that of sound; in another, taste; while, in a fourth, pain and the sensation of a shock are felt. Mechanical irritation excites in one nerve a luminous spectrum; in another, a humming sound; in a third, pain. An increase of the stimulus of the blood causes in one organ spontaneous sensations of light; in another, sound; in a third, itching, pain, &c. A consideration of such facts could not but lead to the inference that the special susceptibility of nerves for certain impressions is not a satisfactory theory, and that the nerves of the senses are not mere passive conductors, but that each peculiar nerve of sense has special powers or qualities which the exciting causes merely render manifest.

Sensation, therefore, consists in the communication to the sensorium, not of the quality or state of the external body, but of the condition of the nerves themselves, excited by the external cause.—We do not feel the knife which gives us pain, but the painful state of our nerves: the

probably mechanical oscillation of light is itself not luminous; even if it could itself act on the sensorium, it would be perceived merely as an oscillation; it is only by affecting the optic nerve that it gives rise to the sensation of light: sound has no existence but in the excitement of a quality of the auditory nerve; the nerve of touch perceives the vibration of the apparently sonorous body as a sensation of tremour. We communicate, therefore, with the external world merely by virtue of the states which external influences excite in our nerves.

By the knowledge of the fact just announced, we are led not only to recognise the peculiar qualities of the different nerves of sensation, in addition to their general distinction from the motor nerves; but we are also enabled to banish for ever from the doctrines of physiology a number of erroneous notions regarding the supposed power of the nerves to perform the functions of each other. It has been long known that blind persons cannot recognise colours with their fingers, *as colours:* but we perceive now why it is impossible for them to do so; and the facts which show us the impossibility of it, afford an explanation of many other circumstances. However acute the sense of touch in the finger of the blind may be rendered by practice, it can still be but the one sense proper to the nerves of the fingers,—*touch.*

The facts which we have considered afford a refutation of opinions still current, according to which it was supposed possible that the functions of the optic and olfactory nerves, when they are absent, can be performed by the nervus trigeminus.

Some animals, though provided with eyes,—for instance, the mole and proteus anguinus,—have been said to want the optic nerves, the sense of vision being then placed in the ophthalmic branch of the fifth nerve. This statement has arisen, in the case of the mole, from inaccuracy of the anatomical examinations; and the same is the case probably in the proteus. The mole has an uncommonly small optic nerve, and a very delicate chiasma, as Dr. Henle has shown to me. It has been stated that, in the cetacea, the office of the olfactory nerve, which, according to Blainville, Mayer, and Treviranus, is extremely small and rudimentary, but still is present,* is supplied by the nasal branches of the fifth nerve. How slight the grounds of this conclusion are, is evident when we consider that we have not the slightest proof that the cetacea have the sense of smell. M. Magendie† imagined that he had found proof of the olfactory nerve not being the nerve of smell, and of this sense being the property of the nasal branch of the fifth. He remarked that, after the olfactory nerves had been destroyed, animals were still sensible to acetic acid, ammonia, oil of lavender, and oil of dippel; for, when these substances were applied, they rubbed their nostrils with their feet,

* Treviranus, Biologie, v. 342.

† Journal de Physiologie, t. iv. p. 169.

and sneezed. This proves, as Eschricht* remarks, and as every one must perceive, that the olfactory nerves are the nerves of the sense of smell only, and not nerves of common sensation; for all the substances which Magendie mentions are excitants of the common sensibility of the mucous membrane of the nostrils, which is derived from the nasal branches of the fifth. The flesh of animals excites the sensation of smell only; and M. Magendie confesses that, when a piece of meat enveloped in paper was placed before a dog in which the olfactory nerves had been destroyed, he did not notice it. That the sense of smell is wanting when the olfactory nerves in man do not exist, or have been destroyed, is shown by the cases related by Rudius, Rolfink, Magnenus, and Oppert, Balonus, Loder, and Serres.† Mery‡ and Berard, on the contrary, state that they have observed persistence of the sense of smell with induration of the olfactory nerves, or of the anterior lobes of the brain. But what assurance have we that these physiologists have not confounded the sense of smell with the common sensibility of the nose?

It was formerly supposed that the auditory nerve was absent in fishes, and its place supplied by the fifth. Even Scarpa and Cuvier believed this: but it has been refuted by Treviranus and Professor J. H. Weber. In some fishes, as the silurus glanis and muræna anguilla, a filament is, according to Weber,§ given off from the fifth to the auditory nerve. There is, however, he says, an accessory nerve of the organ of hearing, which sometimes arises distinctly from the brain, sometimes appears to come off from the fifth or from the vagus, and goes to the ampulla of the posterior semicircular canal and to the sac. In the rays there is a nervus accessorius nervi acustici arising separately from the brain. Buechner‖ states, that in some osseous fishes also the nervus acusticus accessorius, which goes to the sac and the posterior ampulla, is not a branch of other nerves, but a special fasciculus from the medulla oblongata. In the petromyzon, an accessory auditory nerve was observed by Schlemm and D'Alton, going to the labyrinth, and arising from the facial nerve. I observed the same structure in the myxinoid fishes. The circumstance of the accessory auditory nerve arising sometimes from other nerves, must not be regarded as of much importance. In such cases there is probably nothing more than an association of very different fibres in a part of their course, just as in the lingual branch of the fifth in man we must suppose very different fibres—those of taste and those of common sensation—to be associated. Hence also the fact observed by Treviranus,¶ that in

* Diss. de Funct. primi et quinti paris in Olfact. Organo. Magendie, Journ. t. vi. p. 339.

† Compare Eschricht, loc. cit. and Backer, Comment. ad Quæst. Physiol. Traject. 1830.

‡ Hist. de l'Anat. et Chirurg. par Portal, t. iii. p. 603. Magendie's Journ. t. v. p. 17.

§ De Aure et Auditu. Lips. 1820.

‖ Mém. de la Soc. d'Hist. Nat. de Strasburg, t. ii. livr. 2.

¶ Tiedemann's Zeitschrift, v.

some birds the nervus vestibuli is a branch of the facial, is of no physiological importance. In the goose, the nervus vestibuli is a branch of the acoustic nerve itself, the facial nerve merely running closely over it. And in any case, what could the association of fibres of different functions in one sheath prove physiologically?

The nerve of taste appears never to arise as a separate nerve; on the contrary, its fibres seem to be included in other nerves, probably both the lingual and palatine branches of the fifth; for both the palate and tongue are endowed with the sense of taste. Cheese made to touch the palate only, is distinctly tasted. Even the pharynx is the seat of sensations allied to taste, namely, those of nausea.

Loss of taste has been observed in cases where the fifth nerve has suffered from disease.* Magendie observed the same effect after dividing the lingual nerve; and the experiments of Mayo, and those which I myself instituted in conjunction with Professor Gurlt and Dr. Kornfeld, were attended with similar result.

Panizza† regards the lingual branch of the fifth as a mere nerve of common sensation or touch, and the glosso-pharyngeus as the nerve of taste. It appeared to him that taste was not lost after division of the lingual branch of the fifth. The animals in which the experiment was performed, tried to eat bread, milk, and meat, with which colocynth and quassia had been mixed, but immediately rejected them; while, after the glosso-pharyngeus had been divided, they swallowed even bitter substances.

Recent experiments, however, throw doubts upon Panizza's theory.

If taste really remained after the division of the gustatory nerve, it might be due to the palatine branches of the fifth. In experiments instituted by Gurlt, Kornfeld, and myself, the sense of taste remained quite perceptibly after division of the glosso-pharyngeal nerve. Experiments of this kind are attended with difficulty, and are liable to many sources of error. Horses and dogs, if hungry, will eat food impregnated with the most bitter matters, even when all their nerves are in a state of integrity. It is not from the circumstance of their eating or not eating what is bitter, that we can judge of the presence or absence of taste, but from the manner in which they eat it.‡ The results of Dr. Alcock's experiments also [as well as of those of Mr. Mayo and Dr. Reid] were unfavourable to Panizza's theory.

The lingual branch of the fifth is likewise a nerve of touch, or common sensation; the tongue derives its sense of touch from this nerve and from the glosso-pharyngeal. The division of the lingual branch of

* Parry, Elem. of Pathol. and Therap. vol. i. [and Mr. Bishop in the Medical Gazette, Dec. 21, 1833.]

† Richerche Sperimentali sopra i Nervi. Pavia, 1834.

‡ See Kornfeld, De functionibus nervorum linguæ experimenta. Berol. 1836.

the fifth nerve has been observed both by Magendie, Desmoulins, and myself to be very painful. It is possible that there are special filaments for taste and touch associated in it. The chorda tympani, at all events, may be looked upon as a part destined for common sensibility.

The nervous fibres endowed with the sense of taste may be superadded to very different nerves. In birds the nerve of taste is a branch of the glosso-pharyngeal, in frogs it is a branch of the vagus.

M. Magendie* asserts that he has seen nearly all the senses annulled by the division of the trunk of the fifth nerve within the cranium. The loss of vision M. Magendie inferred from the animal not noticing the light of a lamp. But rabbits are frequently not affected by light, even when the fifth nerve is not divided: and M. Magendie himself confesses that, when the light of the sun was allowed to break in where lights had been previously excluded, the eyelids of the animal closed; and this was seen still more distinctly when the light was thrown into the eye through a lens. M. Magendie demonstrates by experiment on animals that which is known too well from the observation of diseases in man, namely, that when the optic nerve loses its power, the fifth does not perform its function,—the perception of light; but he is of opinion that the fifth is at least an auxiliary to the optic nerve, and necessary for the due performance of the visual function. M. Magendie believes also that the fifth is necessary for hearing.

The circumstance of an animal not being susceptible of other impressions immediately after the division of so large a nerve as the fifth, proves nothing more than that it has suffered a serious injury. We know, in fact, that the division of large nerves,—for instance, of the optic nerve,—gives rise to serious symptoms. According to my view, the fifth nerve has no influence either on vision, hearing, or smell. In an epileptic patient, in whom there was inflammation of the eye and opacity of the cornea on the right side, with loss of vision, and subsequently insensibility of the eyelids, nose, and tongue on the same side, deafness of the right ear, and a scorbutic state of the gums, M. Serres found disease of the portio major of the fifth nerve as far as the pons Varolii;† but here the blindness was the consequence of the opacity of the cornea. All the other affections of the senses, as well as the convulsions of the right side of the body, are accounted for by the diseased state of the brain. The inferences which have been drawn from this case are moreover shown to be completely groundless by another case of disease of the whole trunk of the fifth, in which there was insensibility of the entire left side of the head, of the nose, tongue, and eye, while vision remained perfect.‡

* Journ. de Physiol. iv. 302.

† Magendie's Journ. v. 232.

‡ Müller's Archiv. für Anat. und Physiol. 1834, p. 132.

CHAPTER II.

OF THE PECULIAR PROPERTIES OF OTHER NERVES.

Of the nerves of the eye.

We are ignorant as to whether the third, fourth, and sixth nerves have sensitive, in addition to their motor power. Desmoulins asserts that, when they are stretched or pinched, no pain is produced; but it is difficult to determine this with regard to such small nerves, and after the violence that is necessarily done to the animal in laying them bare.

The third nerve supplies the levator palpebræ muscle, the superior, inferior, and internal recti, and the inferior oblique; and from its branch to the latter muscle the ciliary or lenticular ganglion derives its short root, while the long root of this ganglion is supplied by the nasal branch of the fifth nerve, and contains a filament from the cavernous plexus of the sympathetic.

The influence of the third nerve and that of the nasal nerve on the iris deserve a special consideration. Desmoulins relates that, according to the experiments of Fowler, Reinhold, and Nysten, the application of galvanism to the third nerve causes a contraction of the iris. The excellent inquiries of Mr. Mayo have shown that the motions of the iris are regulated by the third nerve through the medium of the short root of the ciliary ganglion, and that the long root of this ganglion derived from the nasal branch of the fifth has no influence over the motions.

The following are the results of his experiments on thirty living pigeons, in which birds M. Muck has shown that the ganglion ciliare has two roots, one from the third, the other from the fifth nerve.

1. When the optic nerves are divided in the cranial cavity of a living pigeon, the pupils become fully dilated, and do not contract on the admission of intense light. (Magendie also observed dilatation of the pupil, and immobility of the iris, as a consequence of division of the optic nerve in dogs and cats; while the pupil became contracted, and the iris immoveable, when the same experiment was performed on rabbits and guinea-pigs.)

2. When the third nerves are divided in the cranial cavity of a living pigeon, the same result ensues; in both these cases the surface of the eyeball retains its feeling.

3. When the fifth nerve has been divided on one side in the cranial cavity of a living pigeon, the iris on that side contracts as usual on the admission of light, but the surface of the eyeball appears to have lost its feeling (which it derived from twigs of the ophthalmic branch of the fifth).

4. When the optic nerves are pinched in the cranial cavity of a living pigeon, or immediately after its decapitation, the pupils are contracted for an instant on each injury of the nerves. (A phenomenon observed by Flourens also.)

5. When the third nerves are irritated in the living or dead bird, a like result ensues.

6. When the fifth nerve is similarly irritated in the dead bird, no affection of the pupil is observed.

7. When the optic nerves have been divided within the cranial cavity of a pigeon immediately after its decapitation, if the portion of the nerves attached to the eyes be pinched, no contraction of the pupil ensues: if the portion adhering to the brain be pinched, a like contraction of the pupil ensues, as if the optic nerves had not been divided.

8. The previous division of the fifth nerves in the preceding experiment produces no difference in the result.

9. When the third nerves have been divided in the cranial cavity of the living or dead bird, no change in the pupil ensues on irritating the entire or divided optic nerves.*

From these experiments we may with confidence conclude that the motor power of the ciliary ganglion and nerves is derived from the third nerve, and that the light does not cause the contraction of the pupil by acting directly upon the ciliary nerves; but that the irritation of the retina and optic nerve acts immediately upon the brain, and from the brain is reflected upon the third nerve and the short motor root of the ciliary ganglion. This might be inferred also from the well-known circumstance that, in an eye amaurotic from paralysis of the retina, the direct action of light does not cause contraction of the iris, but that the iris of this same eye still acts when the light is directed upon the other sound eye. Mayo's experiments show, moreover, that the general sensibility of the eye is given to it by the fifth nerve, the ophthalmic branch of which sends filaments to the conjunctiva, while the long root of the ciliary ganglion from the nasal branch of the fifth supplies the interior of the eye with sensibility. The nutrition of the eye is under the influence of the sympathetic twigs: we have already seen what an influence the sympathetic, by virtue of its connections with the ciliary ganglion, has over the nutrition of the eye; and that, after the superior cervical ganglion has been destroyed, inflammation of the eye with effusion of lymph ensues. M. Magendie found that division of the fifth nerve in rabbits, guinea-pigs, dogs, and cats, was followed by immobility of the iris, with dilatation of the pupil in dogs and cats, contraction of it in rabbits and guinea-pigs.† These effects must depend on a reflected action through the medium of the brain. We can now inquire into the mode in which the third nerve influences the motion of the iris, a point respecting which I have made several original observations. The third nerve, when excited to action, voluntarily or involuntarily, frequently

* Mayo's Anat. and Physiol. Commentaries, 1823, pt. ii. p. 4.
† Desmoulins, Anat. des Syst. Nerv. t. ii. p. 712.

gives rise to contraction of the iris. Since the third nerve supplies all the recti muscles, with the exception of the rectus externus, we know that when the eye is voluntarily directed outwards the third nerve is not active, and that it is so when the eye is voluntarily turned inwards. If one eye be closed and the other turned inwards, we may perceive that the pupil becomes contracted, and that it becomes dilated if the eye be directed outwards, the intensity of the light remaining the same. Hence it inevitably follows that every voluntary motion of the eye in which the branch of the third nerve to the internal rectus is engaged is accompanied by action of the iris; and that, when the sixth nerve is acting, the iris is inactive, the pupil dilated.

If one eye be turned outwards, the other inwards, no remarkable change in the state of the pupil is observed on account of the opposite conditions of the two eyes. If the axes of the eyes are made to converge in a considerable degree, as in looking at a near object situated at the side, or directly in front, the contraction of the pupil becomes very great; on the contrary, the more parallel the direction of the eyes, and the less the internal recti muscles, which are supplied by the third nerve, are determined to action, the wider does the pupil become.

Hence we have voluntary power over the motions of the iris; in other words, whenever the third nerve is excited to action by volition, the iris contracts. Now, in looking at near objects, the axes of the eyes are made to converge,—the eyes are turned inwards; and hence, when we direct our eyes to near objects, the pupil becomes much contracted, and dilates when we look at distant objects. The motions of the iris in birds are not really more subject to the will than in man; the pupil becomes very narrow in birds when we approach them and they become agitated.

It is not, however, the branch of the third which goes to the internal rectus muscle only that has this sympathetic influence over the iris; other branches, and particularly that which supplies the inferior oblique muscle, have the same power. The inferior oblique muscle rotates the eye so as to carry the pupil upwards and inwards: if this movement is executed voluntarily, the pupil becomes much contracted. The eye takes this position involuntarily when sleep is coming on, in sleep itself, in the state of intoxication, and in hysterical attacks; hence we find the pupil contracted during sleep.

The contracted pupil of sleep can, however, be made to contract still more by the admission of intense light, according to the observation of Mr. Hawkins.* At the moment of waking, the pupil, after a few irregular contractions, assumes its usual degree of dilatation.

The facts drawn from *comparative anatomy* are generally confirmatory of the foregoing physiological results. The ciliary nerves are

* Mayo's Commentaries, pt. ii. p. 6.

constantly supplied from the third nerve and nasal branch of the fifth. The following varieties are met with:

1. Branches of the third and nasal nerves unite as roots to form the ciliary ganglion. The ciliary nerves arise in part from the ganglion, and in part from the nasal nerve itself. This is the arrangement of the nerves, according to the extended and accurate researches of M. Muck and Tiedemann in the dog, hare, ox, sheep, goat, deer, roe, hog, owl, pigeon, parrot, goose, turkey, and plover (in the turtle also, according to Bojanus).

2. The ciliary ganglion connected more immediately with the root derived from the third nerve; the ciliary nerves arising from it, going partly to the eye directly, and partly uniting in a looped manner with ciliary branches of the nasal nerve, some filaments of which are continued separately to the eye. This structure has been found in the cat, falcon, heron, raven, cock, duck, merganser, and tern. I regard this form merely as a variety of the former.

3. In the rabbit Muck found no connection of the third and nasal nerves forming roots of a ganglion; both those nerves gave off ciliary twigs separately. According to Retzius, the ciliary ganglion is here situated nearly within the sheath of the third nerve.

4. Desmoulins asserts that the nasal nerve gives off no ciliary branches in the rabbit, guinea-pig, and water-rat; all the ciliary nerves being in these animals derived from the third: he also says that the ciliary ganglion is absent in them, as in all rodent animals. (?)

5. No animal with a moveable iris fails to receive ciliary branches from the third nerve, which is always one of their principal sources when the iris is endowed with motion. M. Muck and Tiedemann asserted, it is true, that in the horse the ciliary ganglion is absent, and that the motor oculi nerve gives off no ciliary branches; but Retzius has discovered a very minute ganglion and its two roots, one derived from the third nerve.* Muck is probably in error, likewise, in stating that in the squirrel, also, none of the ciliary nerves are derived from the third nerve.

6. In fishes the iris is nearly universally immoveable. Muck and Tiedemann found ciliary nerves in the salmo hucho, which arose from the third nerve and from the nasal, and in part anastomosed with each other: in the carp, the ciliary nerves arose from the third pair. From the researches of Prof. Schlemm and D'Alton, it appears that fishes do not differ from other animals in respect to the ciliary nerves, which they found to be generally derived from the usual roots.†

7. In mammalia, the sixth nerve gives filaments to the musculus suspensorius, as well as to the external rectus; and in birds, to the muscle of the membrana nictitans.

8. In cetacea, according to Rapp and Burns, the fifth nerve also gives branches to the muscles of the eye, the special nerves of those muscles

* Isis. 1827, p. 997.

† Müller's Archiv. 1837, lxxviii.

being likewise present. Schlemm and D'Alton found the same to be the case in the petromyzon or lamprey.

9. In the lampreys there are, according to Schlemm, two special nerves for the muscles of the eye; namely, the motor oculi and trochlearis, which unite in the orbit.

10. In the myxinoid fishes, the third, fourth, and sixth cerebral nerves are wanting, as well as the muscles of the eye.

Influence of the brain on the motor nerves of the eye.—Desmoulins and Magendie state that, when the peduncle of the cerebellum is divided in mammalia, the eye of the corresponding side is directed forwards and downwards, the eye of the opposite side upwards and backwards; section of the pons Varolii was attended with the same result.

The fifth nerve.

In the section on the sensitive and motor nerves, we have spoken of the sensitive and motor portions of this nerve, and have shown that its first and second divisions are, in the human subject, sensitive only; that the branches of the third division, which is composed of both motor and sensitive portions, are in part motor, in part sensitive. This important nerve, to which the anterior and lateral parts of the head, and the cephalic tracts of the mucous membranes, (the mucous membranes of the mouth and nose, and the conjunctiva,) owe their sensibility, and the muscles of mastication their motor power, communicates by each of its principal divisions with the sympathetic nerve; and its branches probably receive, through the medium of these communications, organic fibres from the sympathetic.

1. The first connection of the fifth nerve with the sympathetic is that of the nasal branch with the ciliary or lenticular ganglion, which ganglion is connected by a distinct filament with the rest of the sympathetic system. In the ox, the first division of the fifth can be distinctly seen to receive organic fibres from that part of the sympathetic also which is connected with the sixth nerve.

2. The second connection of the fifth with the sympathetic is established by means of the spheno-palatine ganglion, seated on the second division of the nerve, where this is joined by the deep branch of the vidian from the carotid plexus. In the ox, this ramus profundus nervi vidiani, coming distinctly from the sympathetic nerve, gives some fibres to the spheno-palatine ganglion, and many others which accompany the branches of the second division of the fifth nerve. The superficial branch of the vidian, which connects the second division of the fifth with the facial, is of very different nature from the deep branch; it is, according to Arnold, really a branch of the fifth sent to join the facial. Bidder supposes that this nerve is also the means of conveying motor fibres from the facial to the second division of the fifth, which are destined for the muscles of the soft palate. In serpents,

also, the vidian nerve appears to me to give branches to the palatine muscles. In birds, the sympathetic nerve communicates with the first division of the fifth in the orbit, not with its second division, by means of a nerve similar to the vidian. (Schlemm.)

3. The third means of communication between the fifth and sympathetic is the connection of its third division with the otic ganglion.* This ganglion is connected with the third division of the fifth nerve, and yields to it organic fibres which accompany its branches. According to Bendz, the otic ganglion is connected with the organic nerves which come off from the superior cervical ganglion, accompany the external carotid artery, and are continued along the internal maxillary and arteria meningea media.

Two nerves come off from the ganglion for the cavity of the tympanum: one is a branch from the ganglion itself; the other is, as Schlemm pointed out, derived from the internal pterygoid nerve. The latter of these two nervous twigs is the motor nerve of the tensor tympani muscle, discovered by Comparetti; in the calf it passes through the otic ganglion. The other nerve, the nervus petrosus superficialis minor, which arises from the ganglion itself, enters a special canal of the temporal bone in front, and to the outer side of the aqueduct of Fallopius, passes through this canal into the cavity of the tympanum, and joins the tympanic plexus of Jacobson. A small twig leaves it in its course to unite with the facial nerve at its angle. The tympanic plexus, of which the principal loop lies upon the promontory of the tympanum, connects the tympanic nerve of the otic ganglion with the tympanic twig from the carotic plexus of the sympathetic, and the ramus tympanicus of the ganglion petrosum of the glosso-pharyngeal nerve. The last-mentioned branch appears to be given off from the plexus to the glosso-pharyngeal nerve, and to be the means of superadding organic fibres to it.

This whole apparatus, in part constituted of organic fibres, which has its origin in the ganglion oticum, appears to serve the purpose of mingling organic fibres with those of the third division of the fifth, the seventh, and eighth nerves; and to supply the tympanum, and particularly its mucous membrane, with such organic fibres. The otic ganglion appears to be in no way connected with the function of hearing. We may now understand, seeing the number of organic fibres which are interwoven with the fifth nerve, why the division of this nerve was found by M. Magendie to interfere with the nutrition of the eye, gums, and tongue;† and also why there should be such a tendency in the

* Arnold, Über den Ohrknoten. Heidelb. 1828. See also Schlemm, Froriep's Not. 660. Müller, Meckel's Arch. 1832, p. 67. Hagenbach, Disq. circa musc. auris internæ, adject. animadversion. de Gang. Otico. Basil, 1833. Bendz, de anastom. Jacobs. et ganglio Arnoldi. Hafn. 1833; and an account of the description given by earlier anatomists of this ganglion and its nerves, in Müller's Archiv. 1837, p. 284.

† [Would division of the fifth within the cranium, as in M. Magendie's experi-

mucous membranes of the eye, nose, and tympanum to be affected simultaneously in catarrhal affections.

The sub-maxillary ganglion, situated upon the lingual branch of the third division of the fifth, resembles the ciliary ganglion in being composed both of organic fibres, and of fibres of the cerebro-spinal system. Haller, Bock, and Arnold describe it as receiving a filament from the superior cervical ganglion of the sympathetic, which in its course to it accompanies the facial artery. The organic influence of the ganglion on the secretion of the saliva in the sub-maxillary gland may depend on this branch from the cervical ganglion, and on the grey matter of the sub-maxillary ganglion itself. Moreover, this sub-maxillary ganglion receives, according to Arnold, a branch of the chorda tympani, of which the rest continues to accompany the lingual or gustatory nerve. Inasmuch as the chorda tympani is derived from the facial, which is a motor nerve, the filaments which it gives to the sub-maxillary ganglion may account for the motor power of the filaments given by the ganglion to Wharton's duct. Arnold states, that some fibres of the gustatory nerve itself join the ganglion, and from these possibly the gland and its duct derive their sensibility. In reference to its roots, therefore, of threefold nature, this ganglion resembles the ciliary ganglion. According to Prof. Arnold, it gives grey fibres to the gland, to its duct, and also to the gustatory nerve.

The *comparative anatomy of the fifth nerve*, is, we confess, at present but little known; in the higher animals, however, its distribution and physiological properties are nearly the same as in man. It is the principal sensitive nerve of the face. Thus, according to Rapp,* the sensitive fibres which supply the follicles of the vibrissæ or whiskers of animals are derived from the infra-orbital nerve, while the motion of the follicles is dependent on the facial nerve.

When the sense of touch in the snout of animals is very acute, the infra-orbital nerve is always very large, as in animals which have a proboscis.

In serpents and lizards the first division of the nerve appears to me to form its ganglion independently of the second and third divisions. In many animals,—in the cetacea, according to the observation of Rapp and Brunn; in the petromyzon, according to Schlemm and D'Alton; and in the frog, according to Volkmann,—the first division of the fifth gives branches to the muscles of the eye.†

In the frog, a branch of the fifth traverses the cavity of the tympanum, and joins the glosso-pharyngeal branch of the vagus or the glosso-pharyngeal nerve.

In the torpedo, the anterior portion of the electric organ receives a

ments, paralyse the organic fibres which the nerve receives after its exit from the cranial cavity? The implied assertion of the author that such would be the case must be an oversight. See his remarks on effects of division of the vagus, p. 781—782.]

* Die Verrichtungen des fünften Nervenpaares, Leipz. 1832, iv.

† Müller's Archiv. 1837, lvii. lxxix. 1838, 76.

branch of the fifth nerve, while the principal nerves of these organs are branches of the vagus. In the rays, a branch of the fifth nerve goes to the point of divergence of the mucous ducts which radiate out under the skin. In the carp, the vagus, and the last cerebral nerve, by which the muscles of the pectoral fin are supplied, receive a part of their fibres from the fifth nerve.* In the burbot (gadus lota), Weber met with a branch of the fifth to the jugular fin. Prof. E. H. Weber† has discovered that in many fishes, as the silurus and eelpout, there is, in addition to the usual nervus lateralis, which is a branch of the nervus vagus, another nerve derived from the fifth pair, running with the former superficially in the muscles at the side of the body as far as the tail. This ramus lateralis of the fifth is closely connected with the spinal nerves, which is not the case with the branch of the vagus. In fishes, the vagus and fifth nerves are usually the largest cerebral nerves; their developement corresponds to that of the enlargements of medulla oblongata; at the point of origin of the vagus a special cerebral lobe is often developed: the fifth nerve, according to Weber, arises in the carp from an anterior single enlargement; in the silurus, from a lateral enlargement of the cerebellum; in the myxinoid fishes, the lobe of the medulla oblongata terminates anteriorly quite free in the fifth nerve.

The facial nerve, or portio dura of the seventh.

Although the facial nerve contains a certain proportion of sensitive fibres, yet it is the principal motor nerve of the face: its sphere of action extends to all the muscles of the face, those of the ear, and the occipito-frontalis muscle; besides several other muscles, namely, the posterior belly of the digastricus, the stylo-hyoideus, and the cutaneous muscle of the neck. Hence it is the nerve of expression, and also the respiratory muscle of the face, since it is sympathetically affected in all violent or laboured respiratory movements.

Comparative anatomy of the facial.—In proportion as the developement of the muscles of the face, and the expression of the passions in the features, are less perfect, this nerve is of smaller size. In animals provided with a very moveable trunk or proboscis, the facial nerve is very large; and in the elephant, the branch of the facial, which supplies the trunk, is as large as the ischiadic in man.‡ In birds, the office of the facial nerve, as a nerve of expression, does not exist. It serves, however, in some birds still to express the passions, namely, in birds in which the feathers covering the ear are moveable, in which the feathers of the neck can be moved by means of the cutaneous muscle; the muscles which it supplies are only those to which in man it gives

* Weber, Meckel's Archiv. 1827, p. 313.

† De Aure et Aupitu. Lips. 1820, and Meckel's Archiv. 1827, p. 304.

‡ Sir C. Bell's Natural System of the Nerves, p. 127.

branches in addition to the muscles of the face, namely, the muscles which depress the jaw and raise the os hyoides and the platysma myoides. It is, as far as it exists, still a motor nerve; and Treviranus was in error in imagining that in the facial nerve of birds, which he believed to be almost entirely devoid of motor power, he had an example of a nerve altering its function.

In the chelonia (tortoises and turtles), its distribution is nearly the same as in birds. In serpents and lizards, according to my observation, a nerve analogous to the facial passes out close behind the third branch of the fifth, gives a branch posteriorly to join the vagus, and receives, through an osseous canal in the base of the skull, a branch analogous to the vidian, which is connected with the second division of the fifth pair. The trunk of the facial is distributed to the muscle between the os quadratum and inferior maxilla, and in the lizards to the cutaneous muscle.

In frogs, Volkmann has described a nerve, analogous to the facial, which enters the ganglion of the fifth pair, but immediately separates again from it, and is continued as the tympanic branch of the fifth till it joins the laryngeal branch of the vagus. This laryngeal branch of the vagus is given off by the glosso-pharyngeal division of the latter nerve, and this anastomosis of the two nerves may be compared to the similar connection of the facial with the glosso-pharyngeal nerve in the human subject.

In the osseous fishes the facial is not a separate nerve; its fibres are probably contained in the fifth, forming the ramus opercularis of that nerve.

In the plagiostomatous fishes an analogous nerve becomes insulated, and in the cyclostomata the facial is a special cerebral nerve, as Born, Schlemm, and D'Alton have observed in the petromyzon (lamprey); and I have found the same to be the case in the myxinoid fishes.

The *nature of the connection of the facial and gustatory nerve* in man and mammalia *by means of the chorda tympani*, is not at all understood. Cloquet and Herzel describe the superficial branch of the vidian, which comes from the second division of the fifth, as merely applying itself to the facial at the point where it makes an angular bend, being enclosed in the sheath with it; but leaving it again as the chorda tympani, to join the gustatory branch of the fifth. Arnold's researches, however, would make it appear that this view is unfounded, inasmuch as it is not possible without violence to show such a relation between them. Varrentrapp* states that the superficial branch of the vidian, after having joined the facial nerve, does not merely run in the same sheath with it, but gives a part of its fibres to it, so that a part only of the vidian passes over the bend of the facial nerve, without being firmly united with it.

* Observ. Anat. de parte cephal. nerv. symp. Francof. 1831.

The part that is thus continued onwards may, according to Varrentrapp's view, even where it lies with the facial, be regarded as chorda tympani; it may be followed, attached to the gustatory nerve, nearly as far as the sub-maxillary ganglion, where it divides into two branches, of which one enters the ganglion, while the other continues its course in the gustatory nerve. Arnold* says, that where the chorda tympani runs in the sheath of the gustatory nerve, very frequent communicating filaments pass between it and the latter nerve; and that it divides at length into two branches, of which the most delicate enters the sub-maxillary ganglion, the other loses itself in the gustatory nerve. The branches of the ganglion are distributed, as Arnold observed, not merely to the sub-maxillary gland, but also to its duct; it is therefore, in my opinion, most probable that the motion of the duct is dependent on motor fibres of the chorda tympani derived from the facial nerve. Arnold's explanation of the connection of the facial and gustatory by means of the vidian, appears to me not likely to be correct. Arnold has himself indicated the relation of the sub-maxillary ganglion to the motions of the duct of the sub-maxillary gland.

The glosso-pharyngeal nerve.

We have already (at page 650) considered this nerve with reference to its place in motion and common sensation. It supplies the posterior part of the dorsum of the tongue, the papillæ vallatæ, the tonsils, and the pharynx. Whether it also supplies fibres for the sense of taste, is still matter of doubt. The circumstance that the gustatory nerve in birds and some amphibia is a branch of the glosso-pharyngeal, is in favour of such being the case. In the frog, the gustatory nerve is a branch of the vagus. We do not know, indeed, how far the sense of taste extends. The sensations of disgust or nausea, which have their principal seat in the pharynx, are, in a great measure, similar to the sensations of taste; and, with regard to these sensations of nausea, it is doubtful whether they are seated in the pharyngeal branch of the vagus, or in the glosso-pharyngeal nerve.

The tympanic branch of the glosso-pharyngeal nerve ought probably to be regarded as a filament sent from the sympathetic to this nerve. (See pages 609 and 777.)†

Comparative anatomy of the glosso-pharyngeal nerve.—In birds it sends a communicating branch to the vagus, and is finally distributed by one division to the tongue, of which it is, according to Weber, the gustatory nerve; and by another to the superior larynx, a part of this portion descending to the œsophagus. Bischoff also describes a glosso-pharyngeal

* Kopf-theil des vegetat. Nervensyst. Heidelb. 1831, p. 119.

† On the nerves which in birds are the analogue of this branch of the glosso-pharyngeal, see Weber, Anat. Comp. N. Symp. p. 26; and Breschet, in Müller's Archiv. 1834, p. 16.

nerve supplying the tongue in the iguana. In the rattlesnakes, the glosso-pharyngeal nerve, according to my dissections, unites wholly with the vagus, which gives a branch to the tongue. In the frog, the glosso-pharyngeal branch of the vagus is the only nerve analogous to the glosso-pharyngeal. In fishes, there is a branch from the anterior part of the vagus, which, in the carp, is, like the other branches of the vagus sent to the branchiæ, provided with a ganglion, but passes through a special foramen in the cranium, and, besides supplying the first branchial arch, also ramifies in the tongue nearly as far forwards as the opening of the mouth; this has been called the glosso-pharyngeal nerve.

From all these varieties, as well as from the absence of the nervus accessorius in fishes, it is evident that the vagus, glosso-pharyngeus, and spinal accessory form but one common system, the distribution of which may vary very much in the different classes of animals.

Nervus vagus.

This mixed nerve, which acquires its motor influence in a great measure probably by its connection with the inner portion of the spinal accessory (see page 652), is constant in its distribution to the organs of voice and respiration, and to the pharynx, œsophagus, and stomach.

On the vagus depend the sensations of hunger and satiety, and all the various feelings which accompany respiration in health and disease. Brachet* has observed, that the sensation of hunger was no longer felt after the vagus was divided. In a monster, of which the head and thorax were double, and the abdomen single, drink given to the one did not satisfy the thirst of the other, probably on account of the stomach being double.

The vagus nerve contains many organic fibres derived from the sympathetic, which attach themselves in part to the trunk of the vagus, and in part to its branches. To these superadded organic fibres the vagus probably owes its organic chemical influence.

The chemical process of respiration, and the secretion of mucus in the lungs, are probably in part dependent on the influence of this nerve; at all events, the division of the vagus in the neck is followed by the effusion of bloody fluid in the lungs; and, although the chemical process of respiration is at first not essentially disturbed, yet the animals die a few days after the operation,—birds live at most but five or eight days.

The secretion of the gastric juice also is subject to the organic influence of the vagus. The division of the vagus in the neck does not completely arrest the secretion of the gastric juice, but causes it to be formed in less quantity: the effect on digestion is the same; in birds, which live longer than mammalia after the operation, digestion is distinctly performed, but much more slowly than before. The circumstance

* Recherches sur les Fonctions du Syst. Ganglionaire, p. 179. Paris, 1830.

of the chemical processes in the lungs and stomach not being immediately quite arrested, is sufficiently explained by the anatomical fact, that the vagus receives organic fibres, not merely at the upper part of its trunk, but at its lower part also, having there numerous connections with the sympathetic nerve, the influence of which cannot be cut off by the division of the vagus in the neck. The secretion of mucus in the respiratory organs appears to be in all parts under the influence of the organic fibres superadded to the vagus; and therefore it is, probably, that the recurrent nerve, at the point where it makes its turn, receives so many large communicating filaments from the sympathetic.

The division of the vagus on both sides does not arrest the absorption of fluids, or of foreign matters mixed with them, such as poisons, &c. from the stomach (see page 246). The division of the vagus on both sides is fatal in very few days; but the division of one vagus nerve only is not fatal, nor indeed of both, if sufficient time have elapsed before the division of the second for the first to have become entirely reunited. (See page 418.)

The *comparative anatomy and physiology of the vagus nerve* offers many points of interest.

1. In birds and reptiles, in which the nervus accessorius is entirely united with the vagus, the latter nerve gives off one or several branches to the muscles of the neck.*

2. In frogs, a branch from the ganglion of the vagus goes to the muscles of the jaw.† It is the jugular branch of Volkmann, who has shown that its motor influence is derived from a branch of the facial nerve, which has coalesced with it. It is distributed partly to the hyoid muscles, and partly to the muscles of the jaw.

3. The nervus vagus in frogs also gives off a lingual branch, which probably supplies the place of the gustatory branch of the fifth; the ordinary motor nerve of the tongue, the hypoglossus, being present. (Weber.) In fact, this lingual branch of the vagus, when irritated, excites, according to Volkmann, no muscular contractions in the tongue. In serpents and crocodiles, also, this lingual branch of the vagus is present. Bischoff describes another branch of the vagus in the crocodile, going to the muscles of the os hyoides. This also exists in serpents and lizards.

4. The recurrent nerve is found in mammalia, birds, reptiles, and amphibia. Weber has shown that even in the frog a branch of the vagus gives off a filament, which takes a retrograde course to the larynx. The larynx in birds receives a branch from the glosso-pharyngeal nerve, the trachea and inferior larynx have branches from the vagus; but the long muscles which, in many birds, shorten the trachea, receive branches from a special ramus descendens noni. (See page 340.)

* Bischoff, N. Accessorii Anat. et Physiol. Heidelb. 1832; pp. 41, 45.

† Weber, Anat. Comp. Nerv. Symp. p. 44.

5. Volkmann describes a branch of the vagus in the frog, which ramifies in the skin behind the ear.

6. In fishes, the vagus supplies the nerves of the branchiæ, and an intestinal branch for the œsophagus and stomach; in the torpedo and silurus electricus, the nerves of the electric organ also; in the carp, the dental nerves for the palatine teeth; and, in all fishes, the nervus lateralis.

The nervus vagus in fishes evidently acquires increase of substance by its passage through its ganglion: its branches taken together are much thicker than its roots, which, indeed, are not so thick as some of the branches taken singly. In the ganglion the primitive fibres of its roots seem to become divided and multiplied, so as to increase the bulk of the nerve, one primitive fibre in the roots being replaced by several fibres in the branches. In the perch-pike (lucio perca) and silurus, all the branches together form one ganglion; in the carp, the branchial nerves alone form separate ganglia, and thus obtain an increase of substance.*

7. One of the most remarkable branches of the vagus in fishes is the nerve which runs on each side of the body superficially between the muscles as far as the tail, and gives branches to the skin and to the muscles. (?) Desmoulins maintains that this nerve is not a nerve of sensation. But it is certainly not a motor nerve, even though it ramifies in muscles; for, with a battery of forty pairs of plates, I was unable, by galvanism applied to it in the carp, to excite any contractions in the muscles. Van Deen† has discovered this nerve in the tadpole, and in the proteus anguinus. Mayer found it in the menopoma also, and Krohn in the tritons. The short cutaneous branch of the vagus in the frog appears to be the remains of this nerve, or one analogous to it. It has been compared to the nervus accessorius; but I believe that the only corresponding nerve in man and mammalia is the auricular branch of the vagus.‡ The lateral nerve of the lampreys, just like the auricular nerve, is formed both by the vagus and the facial. Since, in the osseous fishes, the facial nerve is included in the fifth, this explains the circumstance of the fifth aiding in the formation of the nervus lateralis in many fishes. In the cyprinus family a branch of the fifth unites even in the cranial cavity with the vagus to form the lateral nerve. In the gymnotus electricus the union takes place outside the cranium. In the silurus and eelpout Weber found the lateral nerves consisting of a branch of the vagus and a branch of the fifth nerve. It is an interesting observation of Mr. Swan,§ that in the cod (gadus morrhua) a branch

* Weber, Anat. Comp. Nerv. Symp. p. 44; and Meckel's Archiv. 1827, tab. iv. fig. 25, 26.

† Müller's Archiv. 1834, p. 477.

‡ Ibid. p. lxxvi.

§ Illustrat. of the Comp. Anat. of the Nerv. Syst. Lond. 1836.

of the fifth nerve, united with a twig from the vagus, gives off two nerves to the trunk; of which one runs along the back over the vertebral column at the base of the fins, the other at the abdominal surface of the tail as far as the caudal fin. Both these nerves communicate with the spinal nerves; the one with their ascending, the other with their descending branches. Here we find, then, a symmetry between the upper and lower half of the tail in the distribution of the nerves, just as there is in the osseous system and in the arrangement of the muscles. Besides these two lateral nerves from the fifth, there are also two branches of the vagus which run over the muscles to the posterior extremity of the body. In the hedgehog, Barkow has described a nerve running along the side of the trunk, and supplying the skin and muscles; but this arises from spinal nerves only, namely, from the last cervical and first dorsal.

8. The branches of the vagus given to the contractile palatine organ in fishes of the genus cyprinus are very remarkable. *

9. In the silurus and carp the vagus gives branches to the thoracic fins. (Weber.)

10. Professor Weber has pointed out that a relation of compensation subsists between the vagus and sympathetic nerves. In serpents, for example, the sympathetic is very little developed, while the intestinal branch of the vagus is proportionally large; in frogs the relation between the nerves as to size is reversed. In fishes, also, the intestinal branches of the vagus are very large; and, in the myxinoid family, the intestinal nerve formed by the union of both vagi extends, according to my observations, as far as the anus, while the sympathetic nerve is absent.

Nervus accessorius Willisii.

The relation of this nerve to the vagus, in respect to the motor power of the latter, we have already discussed. (See page 652.) The spinal accessory exists only in mammalia, birds, reptiles, and amphibia; not in fishes. In birds, reptiles, and amphibia, it forms as it were one root merely of the vagus, since it unites wholly with this latter nerve, which, however, gives off a branch to the muscles of the neck corresponding to the accessory nerve of mammalia. † The sphere of action of the spinal accessory in mammalia,—of that part of it, namely, which does not unite with the vagus,—includes the sterno-mastoid and trapezius muscles. The cause of the singular origin and course of this nerve is not well known. Perhaps it is that the pharyngeal branch given off from the vagus immediately after its exit from the skull, may receive fibres from nearly the entire cervical portion of the spinal cord. There are other nerves also which have an origin of great extent; for example, the ramus descendens noni arises from the hypoglossal nerve, and from the upper

* See Weber in Meckel's Archiv. 1827, p. 309.

† See Bischoff, op. cit.

cervical nerves. The only difference between such cases and that of the spinal accessory is, that the latter nerve is formed within the spinal column, while other nerves do not receive the different fibres composing them until after their escape from the spinal canal.

The hypoglossal or ninth nerve.

The position of this nerve in the cerebro-spinal system has been already determined. It is essentially motor, but has likewise some sensitive fibres. (See page 657.) In some mammalia, according to Mayer's discovery, it has a delicate posterior root with a ganglion. It is the motor nerve of the tongue, and of the large muscles of the neck, which move the larynx.

Comparative anatomy of the hypoglossal nerve.—In birds, this nerve, after being connected by a communicating branch with the vagus, divides into two main branches; by one of which it is distributed to the muscles of the hyoid bone; by the other, to the sides of the œsophagus. In the turkey we have found a long descending branch also, which goes to the long muscle which shortens the trachea. In the turtle and iguana the hypoglossal nerve has been seen entering the muscles of the tongue; in the former animal by Bojanus, in the latter by Bischoff. In the rattlesnake I find a delicate hypoglossal nerve issuing from the skull by a special opening behind the vagus, with which it unites, after being connected with the first cervical nerve. In frogs, the nerve corresponding to the hypoglossal nerve, which supplies the tongue, is derived form the first cervical. This circumstance is intelligible, when we recollect, that even in the human subject the hypoglossal and first cervical nerves are connected. In fishes Weber found that the last cerebral nerve arose by three roots, the posterior having a ganglion; and that it left the cranium by a special foramen, and was distributed to the pectoral fin. In the carp the ganglionic root of this nerve connects itself with a root of the fifth. According to Buechner, the nerve discovered by Weber gives branches to the sterno-hyoid muscle also, and is the hypoglossal nerve: it appears to exist in all fishes; but sometimes, as in the pike and perch, instead of escaping by a foramen in the occipital bone, passes out behind that bone.

If, now, we take into consideration that the first spinal nerve in the human subject has sometimes an anterior root only, and that the hypoglossal in man has only an anterior root, but in some mammalia has a posterior root also, it will be evident that the hypoglossal nerve belongs to the class of spinal nerves, and is as it were the first spinal nerve, which, however, generally passes out through a foramen in the cranium. This consideration renders the analogy between the last cerebral nerve in fishes and the hypoglossal nerve still greater.

Having thus reviewed the varieties in the origin and distribution of the cerebral nerves in different classes of animals, we will now inquire how far it is possible to reduce them to a fundamental type. The idea which must guide us here is that first announced by Meckel, of the division of these nerves into *primitive and derivative*. The *primitive* are the three nerves of special sense,—the olfactory, optic, and acoustic, and the mixed or double-rooted cerebral nerves, which are formed after the type of the spinal nerves, and which may be termed the vertebral nerves of the head. The *derivative nerves* are such as are produced by the separation of a part of the fibres from the root of a *primitive* cerebral nerve, or may become entirely united with the substance of other, cephalo-vertebral, nerves. Meckel has not well carried out this idea, which, as a general principle, is correct. Arnold has made a better application of it. He admits the existence of two vertebral nerves of the head, of which the first is the fifth, with the nerves of the muscles of the orbit and the facial nerve, which were regarded as belonging to the motor portion of the fifth. The second vertebral nerve of the head is formed, according to Arnold, by the vagus, spinal accessory, glosso-pharyngeal, and hypoglossal.* According to my view, there are three vertebral nerves of the head, just as there are three cranial vertebræ. The first is the fifth nerve; the second, the vagus, with the glosso-pharyngeal and accessory nerves; and the third, the hypoglossal. The nerves of the orbital muscles, the third, fourth, and sixth, are derivative nerves, and are to be regarded as the motor portion of the first division of the fifth. In the cetacea, the first division of the fifth gives branches to the muscles of the orbit, the ordinary nerves of these muscles being also present. In the frog, the sixth nerve becomes united with the Gasserian ganglion: here, therefore, the fifth gives branches to the orbital muscles. In the petromyzon, one of the three muscular nerves of the eye—probably the sixth—is wanting; and here, also, the fifth gives branches to the muscles of the orbit.

The facial nerve is certainly a derivative nerve, and resembles very much a motor portion of the fifth; for, in the osseous fishes, it unites into one cord with this nerve, and, as Serres supposed, forms its opercular branch. In the frog, also, it associates itself to the fifth. But the facial has an equally close relation to the vagus; in man and mammalia it is connected with branches both of the fifth and of the vagus. In serpents and lizards it gives a communicating branch to the vagus. In the frog, after being connected with the fifth, it becomes united with a branch of the vagus,—the jugular branch. The facial nerve in the lamprey (petromyzon) forms together with the vagus the nervus lateralis, which in osseous fishes is frequently formed by the fifth and the vagus.

* Consult Buechner, Mém. de la Soc. d'Hist. Nat. de Strasb. and Müller's Archiv. 1837, p. lxxiv.

The second vertebral nerve of the head comprehends the vagus, glosso-pharyngeus, and nervus accessorius. The vagus is in greater part, but not wholly, sensitive; the spinal accessory, in greater part, but not wholly, motor; the glosso-pharyngeal nerve, equally sensitive and motor. [See page 651.]

The third vertebral nerve of the cranium is formed by the hypoglossal nerve alone. In the myxinoid fishes there is the nearest approach to the simple type of the vertebral nerves. The facial is in them the only *derivative nerve.*

The sympathetic nerve.

The physiology of this nerve has been already treated of in different sections of this book; thus, at page 661, its sensitive, motor, and organic properties generally, and, at page 728, the laws of its action, have been investigated. We have here to give an account of its peculiarities in different classes and in individual animals; in doing which, we must, however, confine ourselves to those points which are of physiological interest.*

In birds, the cervical portion of the sympathetic lies in the canal of the transverse processes of the cervical vertebræ; in which situation there is in mammalia, and in the human subject, only a filament of proportionally very small size.

The cerebral nerves with which the sympathetic is most constantly connected, are the vertebral nerves of the head. It is connected with these nerves in fishes at the base of the skull, just as the lateral cords of the sympathetic are connected with the spinal nerves.

In several animals, either certain portions of the sympathetic, or the whole nerve, are replaced by other nerves which differ entirely from its type. As examples we may instance that,

1. In the cyclostomatous fishes the sympathetic is wholly absent, and is replaced by the vagus, which runs along the intestine as far as the anus.

2. In serpents the cerebral portion of the sympathetic is quite separate from the lateral cords of the trunk, and becomes identified with the vagus. The lateral cord of the sympathetic is wanting at the anterior part of the trunk; and, as Weber has observed, branches of the spinal nerves go to the lungs, intestine, organs of generation, and urinary organs. These branches are connected to each other by arched loops, which constitute the only remains of the lateral cords of the sympathetic; and it is to be recollected that such loops very commonly exist between cerebro-spinal nerves. I could find no trace of ganglia in the lateral cord of the sympathetic, except in very large serpents. In these

* For the anatomical details we must refer to the works of Weber, Wutzer, Arnold, Varrentrapp, and Giltay, already quoted; also to Lobstein, De Nerv. Symp. Hum. fabricâ, usu, et morbis; Paris, 1823; and Hirzel, in Tiedemann's Zeitschrift, i.

animals,—serpents,—the vagus extends on the intestine through two-thirds of the abdominal cavity.

3. Even in the higher animals certain portions of the sympathetic are sometimes replaced by other nerves. Thus some glandular organs, instead of being supplied by the sympathetic as we should expect, receive their nerves from the cerebro-spinal system; the lachrymal gland from the lachrymal branch of the fifth; the human mammary gland from the third and fourth intercostal nerves.

SECTION V.

Of the central organs of the nervous system.

CHAPTER I.

THE CENTRAL ORGANS OF THE NERVOUS SYSTEM CONSIDERED GENERALLY.

Functions of the central organs of the nervous system.—The activity of all the functions of the nerves is determined by the central organs, partly under the influence of the mind, and partly independently of this influence. The central organs form the connecting medium between all the nerves, or conductors of nervous influence. They act as excitors, or motors of nervous action, in determining the motor nerves to the production of contraction in muscles; and in this their action may be automatic, or voluntary, as the consequence of incitements of the sensorium commune seated in them; when automatic, their action may be constant or intermittent. Moreover, the central organs have the power either of reflecting the centripetal actions of sensitive nerves upon motor nerves, or of communicating them to the sensorium commune, the seat of consciousness. By the central organs, too, the organic actions of the nerves are maintained in unimpaired power; by them the nervous principle is constantly generated and regenerated; and without them the power and excitability of the nerves as conductors of nervous action cannot be long preserved. This is the general definition of the relation in which the brain and spinal cord stand to the nerves. The correctness of this definition is readily proved by reference to facts already detailed.

1. *The central organs connect all the nerves into one system.*—To this even the sympathetic nerves do not form an exception; for, as we have shown in the preceding section, they are connected at very many points with the central organs by fibres passing from the one to the other. The only difference between the cerebro-spinal nerves and the organic nerves, in their relation to the central organs, is that the former issue much more directly from them; while the organic nerves, although their fibres are in company with the cerebro-spinal nerves brought into communication with the brain and spinal cord, nevertheless have subordinate central organs in their ganglia and plexuses, from which the

organic nervous influence more immediately emanates; still, however, the action of this organic system cannot be long maintained when cut off from its communication with the brain and spinal cord.

2. *The central organs are the excitors of the motor nerves which conduct the motor influence of the nervous principle to the muscles.*—This motor influence may be constant, as we see in the case of the sphincters, the action of which is put an end to by injuries of the central organs; secondly, it may be evidenced in intermittent rhythmic movements, such as those of respiration, which are dependent on the medulla oblongata (see page 348); and, thirdly, this motor influence may issue voluntarily from the sensorium commune of the central organs, this sensorium commune being subject to the spontaneous actions of the mind.

The motor nerves are affected by this motor influence in two ways: the nerves of one class act as mere conductors of it. They are always, it is true, charged as it were with motor power, and can be made to exert a motor action by being merely mechanically irritated; but in the normal state they do not exert this power spontaneously, but only when excited by the central organs; these are the motor nerves of the cerebro-spinal system. The nerves of the other class, which are quite withdrawn from the influence of the sensorium commune, as far as regards voluntary actions, are likewise capable of being excited to constant or periodical action by the central organs; but they present the peculiarity of affording independent discharges of nervous influence, although, after a time, communication with the central organs is found to be necessary for the reproduction of their nervous power: such are the sympathetic nerves with regard to their motor actions. The parts which are subject to the sympathetic nerve, as the heart and intestinal canal, continue to contract spontaneously, even when all communication with the central organs is cut off; but the force and duration of their contractions is entirely dependent on the communication of these nerves with the brain and spinal cord (see pages 192 and 733). During temporary fatigue, as well as during sleep which ensues after the daily action of the nervous system, the influence of the central organs on the peripheral parts of the system is lowered; but this transitory altered state of the brain and spinal cord is not adequate to induce an essential change in the motions of parts subject to the sympathetic system. It is only when the state of exhaustion of the central organs becomes more enduring, when their integrity is essentially impaired, that the motions regulated by the sympathetic nerves become paralysed.

It must not be imagined that during the state of fatigue of the central organs which returns every twenty-four hours, and during sleep, the brain and spinal cord become wholly inactive. The state of fatigue is certainly general, but the sensorium commune, that part of the brain on which the mind acts, is alone reduced to a state of especial inaction;

the voluntary movements only are wholly arrested during sleep. The action of all other parts of the brain and spinal cord is maintained as at other times. This is evident from the sphincters continuing to act, and from the persistence of the rhythmic movements of respiration, both of which sets of motions are dependent on true cerebro-spinal nerves. Certain muscles, therefore, although supplied by cerebro-spinal nerves, continue to act even during sleep; the sphincters are always closed, and in sleep the eye is always turned upwards and inwards, and the iris contracted, so that the pupil is narrow; the mouth, too, is usually closed during sleep. In short, we see that, even in sleep, the whole motor apparatus of the central organs, of the brain as well as of the spinal cord, is in an active state, and that merely the voluntary excitation of this apparatus is absent owing to inactivity of the sensorium commune. We must, therefore, suppose that during sleep the influence of the central organs upon the sympathetic nerve is not interrupted, for otherwise the power of that nerve to maintain certain movements would immediately begin to fail, as is distinctly seen to be the case in apoplexy, in syncope arising from affection of the central organs, and in the experiment of artificially destroying the spinal cord.

3. *Impressions conveyed by the sensitive nerves to the central organs are either reflected by them upon the origin of the motor nerves, without giving rise to true sensations, or are conducted to the sensorium commune, the seat of consciousness.*—In the first case, the centripetal actions of the sensitive nerves merely excite the motor apparatus of the central organs, which has its seat principally in the spinal cord, but of which there are also ramifications in the brain; in the second case, the sensitive impressions are conducted to a particular part of the central organs without exciting reflex movements, and are taken cognisance of in the sensorium commune by the mind. Not unfrequently, both these actions take place; the impressions are perceived by the mind, and at the same time excite reflex motions; the impressions on the sensitive nerves being conducted at the same time to the motor apparatus of the central organs, and to the sensorium commune, as in coughing from irritation in the trachea affecting the sensitive nerves, in the winking of the eyelids excited by a loud and sudden noise, and the contraction of the iris from the impression of light upon the retina. For the theory and laws of these reflected motions we must refer to pages 709 and 736. Since the phenomena of reflection are not dependent on the sensorium commune, but on the motor apparatus of the central organs, and since this apparatus continues in activity during sleep, these motions take place then as well as in the waking state; as is proved by cough from irritation of the trachea, and many other phenomena which occur during sleep.

4. *The organic functions of the nerves are maintained in unimpaired*

force by the central organs of the nervous system.—In this respect the same relation prevails between the sympathetic nerve and the central organs as with reference to the motions of parts subject to the sympathetic. The action of the organic nerves in regulating nutrition and secretion is, in a certain degree, independent. The nutrition of the embryo proceeds, even to the full period, though the spinal cord and brain be destroyed by disease (see page 197).* In some cases, indeed, monsters consisting merely of a part of the body,—the head or an extremity, for instance, in which no heart even was contained, have, nevertheless, been nourished; the blood being conveyed to it by branches of the umbilical vessels, and propelled through it by the heart of another perfect embryo. But, in the adult, nutrition often suffers, although not always, in parts paralysed from disease of the brain or spinal cord; the paralysed parts are more prone to gangrene when injured; and in violent acute affections of the central organs, with a depressed state of their functions, gangrene frequently arises spontaneously in individual parts of the body. In the later stages of tabes dorsalis, the tissue of the penis loses its erectile power, and the generative faculty is lost.

5. *The nervous principle is generated and regenerated in the central organs.*—This is proved by the experiments instituted by myself and Dr. Sticker, which show that the nerves of a limb when their communication with the central organs is cut off, although for a time they possess motor power, yet, if they do not become reunited with their proximal portion, lose, after a few months, all their excitability,—their property of exciting motions when irritated mechanically, or by galvanism; a result from which we must conclude that the constant communication of the nerves with the central organs is necessary for the maintenance of the nervous power of the former, although the central organs still retain their power when their conductors are lost to them. The maintenance of the excitability in the nerves does not however depend solely on the continuance of the influence of the central organs upon them, but also upon their own activity. If a nerve remains for a considerable time in an inactive state, it gradually loses its capability of action. There are small muscles in the human body over which most persons have no power, owing to their not having used them; when the eye is affected with blindness, the optic nerve becomes atrophied from the retina to the brain: Magendie has observed this atrophy of the nerve ensue in birds in a few months after the artificial destruction of vision.

The separation of animal matter which is endowed with life into central organs and other parts dependent on these central organs, is an attribute of all animals; but, more than this, the tendency to this

* Consult also Eschricht, Müller's Archiv. 1834, p. 268.

separation is implanted in the matter of the germ from its origin; and it appears that when this tendency comes into operation, the whole organisation of the germ commences. We have shown at page 43 the probability that all animals, even those apparently the most simple, have nerves distinct from the parts the action of which is dependent on them; and wherever the nervous system is susceptible of anatomical examination, we find it in its turn consist of certain more important central parts and their conductors, the nerves. In the embryo of the higher animals this insulation of parts commences even in the germinal membrane; the portion of the animal matter which is endowed with the powers of the central organs collects in the centre of the membrane, while the parts dependent on the influence of the central organs are formed around. But a similar separation and aggregation of parts goes on in this peripheral portion of the new being, by which are formed the nerves, the conductors of the nervous principle, and the tissues to which they communicate the influence of the central organs.

The formation of the central organs is necessarily attended with the formation of the peripheral parts; and, at the same time that the nerves are formed in these parts, the tissues, which are vivified by their agency, necessarily assume their existence. As soon as this separation between central organs and peripheral parts takes place, the brain and spinal marrow are virtually present; neither exists before this. The formation of the separate regions of the central organs is likewise the result of progressive developement and separation of parts. The separation of the peripheral portion of the embryo into nerves and dependent tissues follows the same law; as soon as the separation commences, the whole nerve is present, the peripheral extremity of the nerve not being first formed, and the rest of it progressively towards the central organs, but the whole of its extent simultaneously. The opposite view, which was adopted by Serres,* is not supported, at least, by any facts; the observations which have been adduced in its support, have not been found correct by Baer, whose researches on the developement of the embryo have acquired a classical value.

If now we compare the lower with the more perfect animals, with reference to the insulation of the central organs from the peripheral parts, and, again, of the central organs of the nervous system from the peripheral parts of this system, we find the insulation of the central organs, although it exists, still incomplete in the animals low in the scale. It would appear that nerves are present in the simplest animals (see page 43). But in them, the nervous principle which gives to the central organs their power cannot be confined to them, but must be possessed by other parts of the nervous system; since the division of these animals into separate fragments does not destroy the organism;

* Anat. Comp. du Cerveau.

on the contrary, gives rise to the production of several distinct beings. This we see very well in the case of some annelida, as the nereides and naides, which have a distinct nervous system; but which may be divided, and the two portions will still live as separate beings. Here, therefore, the vivifying principle of the central organs must be possessed by a large extent of the ganglionic cord. And in the polypifera and planariæ which we may divide in various directions into several portions, each of which continues to live, the matter endowed with the vivifying principle of the central organs must have a much more extended distribution. The tendency implanted in animal matter endowed with life to separate into central organs, and parts dependent on them, is immediately evidenced in the separated portions of the planariæ, just as it is in the germ of the higher animals. It is by the operation of the same tendency that a new animal is formed in both cases. The example of the annelida just adduced, shows that the most essential principle of life does not reside merely in the first or cerebral ganglion of the ganglionic cord, but is present in the whole of the cord; for the vital principle itself is here divisible, together with the living substance of the individual. The question now arises, how far the animals immediately above these possess such a wide distribution of the vital principle through their nervous system.

The articulata, although, like the annelida, they have a ganglionated nervous cord, do not continue to live when thus divided; the insects, however, even present voluntary motions after the removal of their head. A carabus granulatus ran about as before when its head was cut off; and a gadfly (œstrus), when laid upon its back after decapitation, used efforts to turn on its legs. Treviranus mentions an interesting fact observed by Walckenaer relative to the cerceris ornata, a wasp which attacks a bee that inhabits holes. At the moment that the insect was forcing its way into the hole of the bee, Walckenaer decapitated it; it continued its motions nevertheless, and, when turned round, endeavoured to resume its position and enter the hole.*

These facts prove that in the articulata the spontaneous movements which show an adaptation to some purpose do not depend on the influence of the cerebral ganglion alone. The other ganglia are, however, evidently subordinate to the cerebral ganglion in their action.

In vertebrate animals, the spinal cord has not the great influence on spontaneous and voluntary motion which the non-cerebral ganglia of the nervous system in invertebrate animals exert. Even vertebrate animals, however, after decapitation, execute movements which evidence a certain degree of harmony and adaptation. Birds flap their wings; frogs, as Volkmann remarks, resume their sitting posture. I have not myself, however, observed such movements of decapitated frogs,

* Treviranus, Erscheinungen und Gesetze des Organischen Lebens, ii. 194.

which were wholly independent of external stimulus on the principle of reflection, except when the head was separated close to the occiput. When the section was made lower down on the spinal cord, the motions of the frog did not indicate the slightest degree of volition. Though birds still flap their wings when their spinal cord is divided in the middle of the neck, such actions are only grouped muscular motions, which are dependent on the spinal cord, and are very different from voluntary movements.

We are in possession of no facts to prove that the spinal cord, when separated from the brain and medulla oblongata, can be the seat of true sensation. The reflected motions excited by irritation of the surface in decapitated frogs are no proof of this; whenever these reflected movements present any degree of adaptation to a purpose, it is certain that the spinal cord has been divided at its very commencement.

In all the higher and lower vertebrata the mass of the spinal cord in general corresponds to the magnitude of the body which receives nervous influence from it; the spinal cord of a fish is proportionally as large as the spinal cord of the human subject, but the brain increases in size in the higher animals in a direct ratio with the developement of their mental faculties. In fishes, the brain consists merely of several enlargements placed in front of the medulla oblongata. The brain of amphibia and reptiles is larger than that of fishes; that of birds, larger than the brain of reptiles; in mammalia the brain is larger than in birds, and the human brain exceeds all in size. We shall hereafter give the proportional sizes more exactly in numbers. Although all animals, from the infusory animalcules upwards, are equally perfect in their organisation in respect to what is necessary to animal life, yet we must admit a difference in their degree of perfection in relation to intellectual developement and the organs of the mental faculties; a difference which is evidently displayed in the structure of the brain itself.

From the foregoing considerations it is clear that a comparison of the nerves with the central organs of the nervous system (taken together), with reference to their size in different animals, is not calculated to afford any physiological inferences. The size of the nerves compared with that of the central organs will, it is true, on the whole, increase as we descend the scale; but this increase is not great, unless the nerves be compared with the brain alone. The spinal cord, which, besides being a means of communication between the brain and nerves, is a motor apparatus, adapted to the motor powers of the body, appears in all animals to correspond by its mass (not by its length and breadth, which vary greatly,) to these motor powers, and to the nerves which arise from it. The weight of the spinal cord of the burbot (gadus lota), as compared with that of the body of the fish, is, according to

Carus, as 1 to 481; in the land salamander, the spinal cord is to the rest of the body as 1 to 190; in the pigeon, as 1 to 305; in the rat, as 1 to 180; in the cat, as 1 to 161. There are in fishes, it is true, nerves, such as the fifth and vagus nerves, which sometimes actually exceed the spinal cord in diameter. In comparing the nerves and spinal cord in different animals, however, we must regard the thickness of the nerves, but not the thickness of the spinal cord; it is the thickness and length at the same time, or rather the entire bulk of the cord, which must be compared with the aggregate size of all the nerves issuing from it. Moreover, the size of the cerebral nerves, which arise from the prolongations of the spinal cord in the brain, cannot, with any good result, be compared with the size of the proper spinal cord behind the brain.

The foregoing general remarks are intended as introductory to a more exact inquiry into the functions of the brain and spinal cord individually.*

CHAPTER II.

OF THE SPINAL CORD.

The spinal cord is distinguished by its mere anatomical structure from the nerves; it is composed of the same delicate fibres as the brain; it contains in its interior grey substance, the transverse section of which has the form of a cross, the arms or cornua of which are prolonged on each side into the anterior and posterior columns. The two kinds of grey matter and the substantia cinerea gelatinosa of Rolando have been treated of at page 607. But the disposition of the white substance also is peculiar. Rachetti and Rolando have observed that the white substance is divided into lamellæ, which run from without inwards, and which can be seen in sections of the spinal cord that have been kept for a long time in common salt. Rolando moreover maintains that the white substance is formed of numerous longitudinal folds, which lie side by side, thin processes of the pia mater passing from without inwards between these folds, while, from within, thin layers of grey substance are received between them. In the anterior white commissure between

* The most important works relative to the physiology of the brain and spinal cord are,—Gall et Spurzheim, Anat. et Physiol. du Système Nerveux. Paris, 1810. Tiedemann, Anatomie u. Bildungsgeschichte des Gehirns. Nürnberg, 1816. 4. Burdach, Vom Bau und Leben des Gehirns. 1-3. Bd. Leipzic, 1819—26. 4. Carns, Versuch einer Darstellung des Nervensystems und insbesondere des Gehirns. Leipzic, 1814. 4. Desmoulins et Magendie, Anat. des Systèmes Nerveux. Paris, 1824, 2 vol. 8vo. Serres, Anat. Comp. du Cerveau. Paris, 1824, 2 vol. Rolando, Saggio sopra la vera struttura del Cervello e sopra le funzioni del Sistema Nervoso. Ed. 3. Tori o, 1828, 3 vol. 8vo. Flourens, Recherches expérimentales, sur les propriétés et les fonctions du Système Nerveux. Paris, 1824. Treviranus, in Tiedemann's Zeitschrift, Bd. iv.

the two anterior columns of the cord, the white substance, or "medullary membrane," the folds of which form the white substance, passes across from one side to the other. This is not the case in the posterior furrow.

In a physiological point of view, the spinal cord so far agrees with the nerves that it propagates actions of the nerves, which enter it, to the brain, just as the cerebral nerves communicate impressions made on them immediately to the sensorium commune; and that it communicates the influence of the brain to the nerves arising from it, which thus receive, through the medium of it, the cerebral influence, just as if they arose from the brain itself; in other respects, however, the spinal cord differs essentially from the nerves in possessing properties which belong to it as part of the central organs, and do not reside in the nerves. We will consider it more minutely as a conductor, and as a part of the central organs.

1. *The spinal cord as conductor of the nervous principle, or of its oscillations.*—All the cerebral nerves are immediately subject to the influence of the brain, and all the spinal nerves are subjected to the same influence, through the medium of the spinal cord. As soon as the transmission of this influence is interrupted, impressions on sensitive nerves cease to be propagated to the sensorium, and the brain loses the power of voluntarily exciting the motor action of the nerves which are withdrawn from its influence.

The causes which interrupt the communication of the brain and spinal cord with the nerves are pressure upon the nerves, destruction or division of them, and paralysis of their motor power by substances soluble in the fluids of the body, as in poisoning by lead.

When these causes act on a nerve, all its branches which are given off below the affected spot cease to be voluntarily excited to motor action, and the muscles which these branches supply are paralysed with regard to voluntary motion; the action of external stimuli, too, on the same parts produces no sensation.

Those branches, on the contrary, which come off from the nerve above the point of injury, are still subject to the influence of the brain and of volition, and when irritated give rise to sensation; the primitive fibres which compose them being still in unimpaired connection with the brain.

The parts of a nerve below the injured point preserve, however, their motor power for a certain time; it is merely the influence of the brain upon them that is lost. Hence, when a nerve which is paralysed as to voluntary motion, from being withdrawn from the influence of the brain, or cut off from its connection with that organ, is pricked or pinched,—when heat, or a caustic substance, or electricity or galvanism, is applied to it,—no sensation is excited, it is true; but the muscles to which the nerve sends branches are excited to contraction. The nerve does not

lose this excitability until it has been several months cut off from intercourse with the brain.

In man and the higher animals the spinal cord stands in the same relation to the brain as all the cerebral nerves; it is to be regarded as the common stem of the nerves of the trunk, although it is, besides this, distinguished before the nerves by special properties.

Let us compare with this statement the consequences of injuries to the spinal cord. Lesion of the lowest portion of the spinal cord induces paralysis of the inferior extremities of the rectum and bladder; if the lesion is situated at a higher point of the cord, the abdominal muscles are paralysed in addition; if at a still higher point, the thoracic muscles also: lesion of the spinal cord in the cervical region, but below the origin of the fourth cervical nerve, paralyses all the parts before mentioned, and the arms likewise, but not the diaphragm; for the phrenic nerve arises from the fourth cervical nerve: injury to the medulla oblongata paralyses the whole trunk. When the lesion of the cord extends progressively from below upwards, the paralysis of the body extends in the same manner from the lower to the upper parts, as we observe in tabes dorsalis. The spinal cord thus presents every resemblance to a common trunk of the nerves of the body, in the effects of lesion of it in producing paralysis. Moreover, if we irritate the upper part of the spinal cord mechanically, or by galvanism, all the muscles of the trunk are thrown into contraction, just as the muscles which receive branches from a particular nerve are made to contract by irritating the stem of the nerve. Again, if we divide a nerve, the portion cut off from communication with the brain still retains the faculty of exciting, when irritated, contractions in the muscles to which it is distributed; and, in the same way, if we divide the spinal cord in an animal, the part withdrawn from the influence of the brain will, when irritated, still excite the nerves which arise from it to action, and thus the muscles to contraction.

But the spinal cord does not merely represent in the brain all the nerves of the trunk in the aggregate, but also all the individual primitive fibres of these nerves singly; for affection of certain parts of the spinal cord interrupts the transmission of nervous influence to certain muscles of the trunk only, and lesion of certain parts of the brain paralyses only certain parts of the body. A cause of paralysis affecting only one side of the brain and spinal cord gives rise to paralysis of one side of the trunk only; and the less extensive the lesion,—the less it embraces of the columns of the spinal cord,—the smaller is the number of parts which are deprived of the influence of the brain. If, moreover, we consider that it is the action of the brain which regulates the number of muscles that are called into action in every voluntary motion, it will appear to be a necessary inference that the primitive fibres in the

spinal cord do not unite with each other, but continue their separate course as in the nerves, so as to communicate isolated sensations to the brain, and to transmit from the brain the stimulus for isolated motions; for, if the nervous fibres coalesced in the spinal cord, neither a local isolated sensation nor an isolated contraction of separate muscles would be possible. Irritation of certain parts of the brain and spinal cord gives rise also to muscular spasms, or to sensations in isolated parts of the trunk.

The primitive fibres, as they issue from the spinal cord, are not already arranged into separate nerves; but the nerves are formed by the radicle fibres being collected into fasciculi. The anterior and posterior roots of the nerves are, it is well known, inserted into the anterior and posterior columns, at a little distance on each side of the middle line. The fasciculi which form the roots of the nerves of the cauda equina are inserted close to each other in an uninterrupted series; the origins of the rest of the nerves appear externally, where the radicle fasciculi pierce the pia mater, to be a little distant from each other. But, when they are traced still deeper, the fibres are found to spread out still more, and to form a tolerably continuous line of insertion, the root of each spinal nerve being formed by a certain number of the radicle fibres being collected together into one bundle. We may, therefore, regard the spinal cord as a trunk formed of nervous fibres, which sends out, anteriorly and posteriorly, in uninterrupted series, many millions of primitive fibres of motor and sensitive endowment to all parts of the body; these fibres being between their origin and their peripheral termination collected into numerous large and small fasciculi by means of cellular sheaths.

With respect to the relation which exists between the nerves and spinal cord, comparative anatomy affords us no information. The proportional length of the spinal cord varies very much. The hedge-hog, in which the panniculus carnosus requires a considerable supply of nervous influence, while the skin, armed with spines, is little susceptible of sensitive impressions, has so short a spinal cord that the posterior half seems to be wanting: in most other mammalia the cord extends nearly the whole length of the vertebral canal; and in rabbits and guinea-pigs, although the tail is so short, it reaches beyond the sacral vertebræ; * which shows that its length does not depend solely on the length and size of the tail. In the kangaroo, in which the great tail serves rather as an organ of support than of touch, the spinal cord is, according to Desmoulins, not longer than in dogs: while in apes with prehensile tails it is said to extend, still of considerable size, as far as the vertebræ of the sacrum. In the tetrodon mola—a fish which is almost as high as it is long—the spinal cord appears at first sight to be entirely absent. The

* Desmoulins, op. cit. ii. p. 539.

brain is prolonged into an extremely short wedge-shaped spinal cord, from which the roots of the nerves arise anteriorly and posteriorly in a continued series. In most animals (and this is particularly evident in fishes and chelonian reptiles) the spinal cord does not gradually diminish in size, in proportion as it gives off the nerves; but is, at its inferior extremity, nearly as thick as it is at its upper part.

The discovery that the anterior roots of the spinal nerves are motor, and the posterior sensitive, (see page 640,) has thrown great light on the different kinds of paralysis. We know that in some cases the sensibility of a limb, or of one whole side of the body, or of the lower half, is lost, the power of motion remaining unimpaired; that in other cases the sensibility is perfect, and the power of motion only lost; and again, that in a third order of cases the paralysed parts are deprived of both motion and sensation. Now we are naturally led to inquire whether the same difference as to motor and sensitive power, which distinguishes the roots of the nerves, prevails also in the spinal cord; do the motor and sensitive fibres run separately in the spinal cord to the brain? The difference in the various cases of paralysis seems to show that such is the case; for the remarkable pathological facts above mentioned cannot otherwise be explained. But it is another matter to determine which are the motor, and which the sensitive parts of the spinal cord. It may be supposed that the anterior columns from which the motor roots arise are themselves motor, and the posterior columns from which the sensitive roots arise merely sensitive, throughout the whole length of the spinal cord; or it may be questioned whether the white substance of the cord be not endowed with the one function, the grey substance with the other. In favour of the first supposition, which is that adopted both by Sir C. Bell and by M. Magendie, no satisfactory proofs have been adduced either from experiment or disease. It is impossible to determine it by experiment; for, in dividing the posterior columns, the experimenter necessarily subjects the anterior columns to pressure. The anterior and posterior columns cannot indeed be shown to be anatomically distinct.* Magendie† stated, as the result of his experiments, that the posterior columns were very sensitive; that the anterior were on the contrary not sensitive, but that violent contractions of muscles took place when they were irritated. He afterwards‡ admitted, however, that such a difference between the anterior and posterior columns was not absolutely proved by the experiments. Backer§ observed loss of motion only after division of the anterior columns, loss of sensation from division of the posterior columns; nux vomica excited in animals,

* I gave this as my opinion in my memoir on the roots of the nerves in the Annal. des Scienc. Nat. 1831.

† Journal de Physiol. t. iii. 153.

‡ Ibid. p. 368.

§ Comment. ad Quæst. Physiol. Ultraj. 1830.

of which he had divided the anterior columns of the spinal cord, no convulsions of the posterior extremities. Seubert's experiments afforded him a decisive result with respect to the roots of the nerves, but not with regard to the spinal cord. They seemed to show that the more anterior portion of the cord transmits principally, but not solely, the motor influence; the posterior principally, but not solely, the sensitive influence. These results agree with those obtained some years since by Schoeps.* According to the experiments of the last observer, section of the anterior columns diminishes the sensitive power, but in a less degree than section of the posterior columns, which on the other hand puts a stop to the motion of the extremities, but only for a time, while section of the anterior columns permanently arrests the movements. The cases of paralysis collected by Seubert† are only in part confirmatory of the hypothesis which we are considering; several are directly opposed to it, as is likewise the circumstance that the nervus accessorius (a motor nerve) arises in birds and reptiles wholly from the posterior columns. Bellingeri‡ maintains that the posterior roots of the nerves have a threefold origin; namely, from the posterior cornua of the grey matter, from the white substance of the posterior columns, and from the lateral columns: that the anterior roots of the nerves, on the contrary, arise from the anterior columns, from the anterior lateral furrows, and from the lateral columns. If this statement be correct, which is very doubtful, the posterior roots would alone be connected with the grey substance.§ Bellingeri supposes, without any grounds, that the internal grey substance is the seat of sensation, the white of the motor power; and that the anterior columns of the spinal cord, and the anterior roots of the nerves, supply the flexor muscles, the posterior the extensors: this is at all events incorrect with regard to the roots of the nerves. According to Prof. E. Weber,‖ it is sometimes possible to trace the roots, both anterior and posterior, to the grey substance:¶ Rolando doubted this.

No experiments, unfortunately, can be instituted likely to determine the share which the white and grey substances have in the functions of motion and sensation; and what renders all experiments on the anterior and posterior columns uncertain, is the property which the spinal cord possesses of reflecting sensitive impressions on the motor apparatus.

* Meckel's Archiv. 1827.

† De funct. rad. ant. et post. Nerv. Spin. Carlsruhæ, 1833.

‡ De Medullâ Spinali. August. Taurin. 1823.

§ [In the ox, Bellingeri was able to trace fibres from the anterior root also to the grey substance of the cord.]

‖ Hildebrandt's Anatomie, Bd. iii. p. 374.

¶ [Mr. Grainger also has satisfied himself by repeated examinations that each root of the spinal nerves is connected both with the external fibrous part of the cord and the internal grey substance. (See his work on the spinal cord, p. 34.) The application which he makes of the fact has been already mentioned in a note at page 721.]

Even supposing, for example, that the anterior columns were solely motor, and the posterior sensitive, an injury to the posterior columns would nevertheless be very likely to excite muscular contractions by virtue of its secondary influence on the anterior columns; all severe lesions of the cord throwing it into the peculiar state in which any irritation of a sensitive nerve propagated to it is reflected upon motor nerves. (See page 711.)

The fibres of the spinal cord pass through the medulla oblongata to reach the sensorium commune. All the primitive fibres of the nerves terminate in the brain; those of the cerebral nerves immediately, those of the spinal nerves through the medium of the spinal cord. The brain (we do not here inquire into the properties of its different parts) receives the impressions of all the sensitive fibres of the body, becomes conscious of them, and recognises the seat of the impression according as different primitive fibres are affected; the brain, on the other hand, excites the motor power of all the motor fibres, and of the spinal cord, giving rise thus to the voluntary motions. In this action of the brain we can but admire the infinitely complicated and delicate mechanism, though the powers by which it acts are wholly unknown to us. And different as they are in other respects, we can but perceive in the action of the brain, when it calls into activity a certain number among the infinitely numerous primitive nervous fibres, a similarity to the play of a many-stringed instrument, the strings of which vibrate when the keys are touched. The mind is the performer or excitor; the primitive fibres of all the nerves which spread out in the brain are the strings; and their cerebral extremities, the keys. Niemeyer* supposes voluntary motions to be the result of the tension of the antagonistic muscles being arrested.

The spinal cord resembles the nerves again in the sensations produced by any affection of it being referred to the extreme parts. Pressure on a nerve gives rise to the sensation of creeping in the skin; pressure also on the spinal cord causes the same sensation to be felt in all the parts which receive their nerves from it below the seat of the lesion. Division of nerves, or tumours of them, cause severe pain in all the parts to which the nerve is distributed; in the same way inflammatory and other affections of the spinal cord are often attended with severe pains in the extreme parts of the body. Even when there is perfect insensibility to external stimuli, lesions of the spinal cord may still excite sensations which are referred to the peripheral parts. Thus, in cases where the lower extremities are completely deprived of motion and sensibility, the sensation of creeping may still be felt in them.† The sensations in these paralysed parts may indeed amount to severe pain, as in

* Materialien zur Erregungs-theorie. Gött. 1800.

† See Ollivier, De la Moëlle Epinière, et de ses maladies. Paris, 1823.

the case of the patient, Heydenreich, at Bonn, already mentioned (page 692). The sensation of creeping of ants over the surface is, however, the most frequent symptom in affections of the spinal cord, and is indeed scarcely ever absent. It is analogous to the tinnitus aurium in the auditory nerve, and the muscæ volitantes and other morbid phenomena of vision; and, since the motion of the blood in the retina of the healthy subject gives rise to the appearance of points flying about whichever way the eye is directed, this feeling of creeping of insects or of the running of points over the surface is probably the effect of the motion of the blood in the capillary vessels of the diseased part of the spinal cord. In some instances, in place of the creeping sensation, there has been an incessant itching of the legs, which could not be removed by scratching.* The aura epileptica is another similar symptom of affection of the spinal cord.

Since the true seat of sensation is not in the nerves, nor in the spinal cord, which merely transmit the necessary currents or oscillations of the nervous principle to the sensorium commune, in which the sensation is really perceived, it is easy to conceive why the same sensations should arise from irritation of the fibres of the spinal cord, or of the nerves, at very different points of their length; for each nervous fibre, however long, can act on the sensorium by its cerebral extremity only, at however many different points of its length it may be irritated. The same apparent contradiction, however, is met with here in the case of the spinal cord as we found apply to the nerves, namely, that pain is not merely felt in all the parts which receive nerves from below the seat of the lesion, but that the injured or diseased part itself is painful. There are many cases of pain about the spine which are not instances of this; diseases of the spinal column itself namely, and of the membranes of the cord, are necessarily attended with pain, while they may by producing pressure on the spinal cord give rise to the usual symptoms in the extremities. But there are instances of pain really affecting the spinal cord itself,—rachialgia. The sensations of rigour and cold trickling down the back must also be seated in the spinal cord. We are at present ignorant why sensations should at one time be felt in the peripheral parts, at another in the spinal cord itself.

We have hitherto considered the points of similarity between the nerves and the spinal cord, regarding the latter as a conductor of the nerves arising from it to and from the brain; we will now inquire into those properties of the spinal cord which distinguish it from the nerves, and which it enjoys as a part of the central organs.

2. *The spinal cord, as a part of the central organs of the nervous system.*—The anatomy of the spinal cord is alone sufficient to show that it is not merely a conductor of the nerves to the brain; if it were such, it would, like any other nervous trunk, consist at its upper part merely of the aggregate of the nerves which it gives off at the different points of its

* See Ollivier, De la Moëlle Epinière, et de ses maladies. Paris, 1823.

length, and it would diminish gradually in size from above downwards in proportion as the nerves leave it, and form a regularly tapering and pointed cone. But although, on the whole, it does become smaller from above downwards, yet, at its extremity, where it gives off the last nerves, it is of greater bulk than would be formed by the fibres of those nerves: moreover, it presents enlargements opposite the origin of the nerves of the extremities, and in fishes it forms at its lower end a club-shaped enlargement pointed below.* Further, the spinal cord is formed, like the brain, of two distinct substances.

But the properties and functions also which distinguish the spinal cord from the nerves, can be distinctly indicated.

a. The spinal cord has the property of reflecting sensorial irritations of its sensitive nerves upon the motor nerves. This property, by virtue of which a sensitive impression gives rise to motions, although there is no communication between the primitive fibres of the two kinds of nerves, has been treated of in the chapter on reflected motions. No nerve separated from the central organs of the nervous system has this property. The reflecting action of the spinal cord and medulla oblongata is a function of the healthy state, yet in a limited degree. But in animals the disposition to this action in the spinal cord is much increased by the influence of narcotic poisons and by decapitation, particularly in reptiles and amphibia. If we cut off the head of a land salamander (salamandra maculata), the trunk remains standing on the feet, and the body now writhes as soon as the skin is irritated or merely touched. This property is retained for several hours by every separated portion of the body in which any part of the spinal cord is left. If the animal be cut in two, the lower portion can be excited to motion as well as the upper portion; the tail may be divided into several segments, and each segment in which any portion of spinal cord is contained contracts on the slightest touch; even the extremity of the tail moves as before, as soon as it is touched. All the portions of the animal in which these movements can be excited, contain some part of the spinal cord; there is in this animal no proper cauda equina. The spinal cord is evidently the cause of the motions excited by touching the surface; for they cannot be excited in parts of the animal, however large, if no cord is contained in them. Mechanical irritation of the skin excites not the slightest motion in the leg of the salamander when it is separated from the body; and, nevertheless, the extremity of the tail moves as soon as it is touched.

The sensorial impression communicated to the spinal cord excites in the decapitated salamander motion, not merely of the parts immediately subjacent to the part of the skin irritated, but of the whole body, even when merely the tip of the tail is irritated. The spinal cord, therefore, in these animals has properties entirely different from those of a nerve; for a nerve when separated from the central organs is not susceptible of

* E. H. Weber, Meckel's Archiv. 1827, p. 316.

sensation, and cannot be excited to the production of motions by irritation of a sensitive nerve of the skin.

b. The spinal cord has the property of reflecting the action of sensitive nerves upon motor nerves, without itself perceiving the sensation. The movements of near and distant parts of the body excited in decapitated animals by irritating the surface of the body, have been adduced as proof that the spinal cord is in part the seat of the sensorium commune, but they are fully explicable by the property possessed by the spinal cord of reflecting the centripetal action of a sensitive nerve upon motor nerves. We have already shown, in the chapter on reflected movements, that the action of the sensitive nerve is most prone to be reflected on the motor nerves which arise near the same part of the spinal cord; and we cannot be surprised, therefore, that irritation of the skin of the foot excites retraction of the foot; irritation of the skin of the arm, retraction of the arm. An equally involuntary action of the irritated parts is excited in our own persons by a severe burn, and by irritation of the mucous membrane of the pharynx, larynx, and trachea. The retraction of the extremities in a decapitated frog, when the skin is irritated, takes place, therefore, equally as independently of consciousness and volition, as the general tetanic spasm excited by touching the skin in a decapitated salamander or a frog poisoned with a narcotic substance. Moreover, reflected motions are excited during life in the human body, quite independently of consciousness. In the movements of the muscles of the trunk which attend vomiting, and which are excited by a morbid state of the stomach, intestine, kidney, liver, or uterus, the irritation in these different organs is very frequently, and generally indeed, not felt; that is to say, the centripetal excitement of the sensitive nerves, which is propagated to the spinal cord and medulla oblongata, does not act on the sensorium commune. And thus we see distinctly that the reflex action of the spinal cord is not necessarily attended with sensation or perception of the sensitive impressions, and that the arguments adduced from the reflected actions for the existence of consciousness in the spinal cord are unfounded. The head, also, when separated from the trunk, may exhibit the phenomena of reflected motion, although it is not in the slightest degree probable that the head of a man, or one of the higher animals, is, when separated from the trunk, capable of conscious perception. The loss of blood accompanying decapitation, independent of the other effects,—such as the division of the upper part of the medulla,—is greater than any which usually deprives the human subject of consciousness. The contraction of the muscles of the face, when the stump of the spinal cord in the head of a decapitated criminal is irritated, is no more than must necessarily occur: we should not indeed be surprised if reflected motions were excited by merely irritating the skin of the head separated from the trunk; for this would be the same phenomenon as those observed in the separate portions of the salamander, and

would be explicable in the same way as the fact that, if in the head of a young kitten separated from the trunk we introduce the finger into the pharynx, it is embraced firmly, the pharynx contracting as if to swallow.

c. The spinal cord is a motor apparatus which, even when separated from the brain, and without any external stimulus, can excite automatic movements. The nerves, at all events those of the cerebro-spinal system, have not this power, although the motor action of the sympathetic system in this respect resembles that of the spinal cord (see page 732). A cerebral or spinal nerve no longer in connection with the central organs is incapable of exciting motions in muscles, unless it be itself irritated; the spinal cord, on the contrary, can still emit motor influence to the muscles, even when its communication with the brain is severed. The land salamander continues standing on its feet after its head is cut off. The body of the frog sometimes moves after decapitation, drawing up or extending a limb; though this is not always observed—very frequently the animal lies quite motionless. An eel moves for a considerable time after it is deprived of its head. In experiments on the amphibia and reptiles, it is necessary to be very cautious; if the section be made too high up, a part of the medulla oblongata will be left connected with the trunk, and then the body may present not merely automatic but voluntary movements, such in fact as we observed in the upper part of the body of a frog divided below the head, when in the upper half perception and volition are present, and in the lower half absent. Another circumstance, to which Dr. Marshall Hall has directed attention, and which merits great consideration, is the following. Reflex phenomena are very readily excited in a snake after decapitation; a slight touch is sufficient to induce motions, and these motions bring new points of the surface in contact with the table or other objects, thus renewing the stimulus. The animal at length becomes quiescent; but a slight shock or touch is sufficient to re-excite the movements.

d. The spinal cord, although capable of exciting the motor nerves to automatic actions, nevertheless, in the healthy state, leaves a great part of the motor nerves, those supplying the muscles of locomotion more especially, in a quiescent state; while on many others it exerts a constant motor influence; maintaining thus constant involuntary contractions, which are arrested only by the spinal cord becoming paralysed. The motions of this kind are,—1. those of muscles which are also subject to the influence of the will, as the sphincter ani; 2. those of muscles not subject to the influence of the will, as the sphincter vesicæ urinariæ, the muscular coat of the intestines, the heart, &c. For these actions the spinal cord must possess a special apparatus more independent of the sensorium commune than that part of it which is engaged in the voluntary actions; though this cannot be demonstrated anatomically. The communication between the brain and spinal cord may indeed be interrupted in the lower animals, without the motor influence of the spinal

cord upon the sphincters being arrested; thus Dr. Hall observed, in the turtle, that the sphincter ani continued closed after decapitation, and did not relax until the removal of the spinal cord.

e. The spinal cord has a great tendency to propagate a particular state of one part of it to other parts; in this property it differs entirely from the nerves. A nerve does not so readily communicate a change in its state, such as is produced by galvanism, to the whole spinal cord, provided the spinal cord itself be not irritated. If the anterior or posterior root of one of the last spinal nerves be divided in a frog, and the portion left connected with the spinal cord galvanised by means of a single pair of plates, the stimulus is not communicated readily through the spinal cord to the anterior parts of the body; no contractions of the muscles about the head are produced. But if the extremity of the spinal cord itself be irritated in the same manner, the muscles of the anterior part of the body are thrown into action. I performed the experiment thus: I separated all the roots of the nerve close at their origin from the spinal cord, as far forward as opposite the anterior extremities, so that I could raise up the posterior part of the cord, and could place a plate of glass beneath it. Then, on connecting both poles of the galvanic apparatus with the end of the cord, contractions were produced in all the parts still connected with the cord by nerves. This property enables us to understand how a disease which has its seat originally in the inferior part of the spinal cord, gradually affects the upper parts of the trunk, and even the head; how, for example, it happens that exhaustion of the lower parts of the spinal cord, induced by debauchery, may be attended with imperfect vision or amblyopia, tinnitus aurium, and other symptoms.

f. The spinal cord when in a state of great irritation, whether this arise from inflammation, from violent irritation of nerves (as in traumatic tetanus), or from the action of narcotic poisons, emits a constant motor excitement to all the voluntary muscles. The tension, which, in the sound state, it exercises only over the sphincters, is now general: convulsions of the whole body ensue; or tetanic cramps, which recur from time to time, and are even constant in many muscles, as those which move the jaw. The affection is sometimes acute, as in the cases already mentioned; sometimes chronic, as in epilepsy; and the exciting irritation may in this case also be seated in the central organs themselves (epilepsia cerebralis or spinalis), or in particular nerves, as in epilepsy from tumours on nerves. A similar state of irritation of the spinal cord, but slighter in degree, giving rise to intermitting movements, is observed in the diseases attended with chronic spasms, as chorea, &c.

g. When animals are poisoned with narcotic substances which give rise to convulsions, the spinal cord, and not the nerves, are the source of the motor influence that excites the movements. If the nerves of an extremity be divided before the nux vomica or strychnine is introduced

into the system, no cramps are produced in that part. If, before or after the animal is poisoned, the spinal cord be cut across, the cramps nevertheless take place in the parts supplied by the lower half of the cord. (See page 629.)

h. The *force* of our voluntary movements is also dependent on the motor tension of the spinal cord. The intensity of our muscular efforts is in a great measure dependent on it. The greater part of the motor nerves are, it is true, excited to action, not by the spinal cord, but only by the influence of the will, and when this is not in operation they are left in a quiescent state; but nevertheless the force and duration of the motor actions excited in these nerves by the sensorium commune are determined by the spinal cord. The cord is always charged, as it were, with motor power, and, although in transmitting the nervous fibres from the brain, it acts as a conductor of the oscillations originating in the sensorium commune, still the intensity of the action excited depends not merely on the strength of the will, but also on the amount of motor power accumulated in the cord. Hence this part of the central organs may retain its property of conducting the volition from the brain, but lose the second power by which it determines the strength of our movements; and this is what happens in tabes dorsalis, a disease caused only by debauchery, and attended with atrophy of the cord. Here no muscle of the lower extremities is at first paralysed; all obey the influence of the will, even in the advanced stages of the disease,—the patient can execute every movement, and it is evident that the spinal cord is still unimpaired as a conductor of the oscillation or current originating in the sensorium. But the force of the movements is lost; the patient can neither stand nor walk for long at a time; and the power gradually diminishes until the paralysis is complete. This kind of paralysis must be carefully distinguished from others, in which the conducting property of the cord is injured at one point, and muscles which receive their nerves from below that point are no longer subject to volition, while all other muscles retain their full power of motion.

i. The spinal cord is the source of the sexual power; the exercise of the sexual function depends on it. The spinal cord is incontestably the part of the nervous system most affected in the act of coitus; this is evident from the energetic reflected motions excited by the irritation of the sensitive nerves of the penis, the contractions of the vesiculæ seminales and perinæal muscles. The state of exhausted muscular power which follows the act must have its source in the spinal cord. The degree of tension of the nervous power of the cord which is necessary for the sexual appetite is only gradually regained, and then ensues that state in which erection of the penis is excited every time that the mind is directed to objects relating to the sexes; the impression on the sensorium causing such a discharge, as it were, of force accumulated in the spinal cord as gives rise by the organic nervous influence to the accu-

mulation of blood in the penis. This sexual potency is also lost in diseases of the spinal cord.

k. The influence exerted by this organ upon the organic chemical processes of the capillaries, through the medium of the organic nerves, is evidenced not only in the altered state of the cutaneous secretion in syncope, but still more clearly by the condition of the skin in men in whom the spinal cord has become affected in consequence of sexual excess. In these cases there is not merely general loss of power, but also diminished turgescence of the skin, diminished perspiration, dryness of the skin, and defective generation of heat; the feet, hands, and genitals are cold.

l. The spinal cord is also the subject of a morbid impression in all febrile affections; and the peculiar alteration of the sensations and motions and of the organic processes, the secretions and generation of heat, in fever can only be accounted for by the influence of such an organ as that which we have been considering in this chapter. Since affections of the cerebro-spinal nerves do not usually give rise to fever, but rather to other affections of the nervous system, and since fever is most frequently excited by altered action of the capillary vessels in some part of the body,—whether such as attends affections of the mucous membranes, or inflammation of some organ,—it is not very improbable that such an impression as would be produced by severe lesion of the organic nerves in any part of the body (whether from inflammation or other cause of irritation) is in fever propagated to the spinal cord, and thence reflected upon all the nerves of the body.

With regard to the organic actions of the spinal cord as compared with the brain, it has been shown by the experiments of Flourens, which Hertwig* has confirmed, that a bird after the cerebral hemispheres have been removed will, if food is forced into its mouth, continue to be nourished for a considerable time,—will not become emaciated.

CHAPTER III.

OF THE BRAIN.

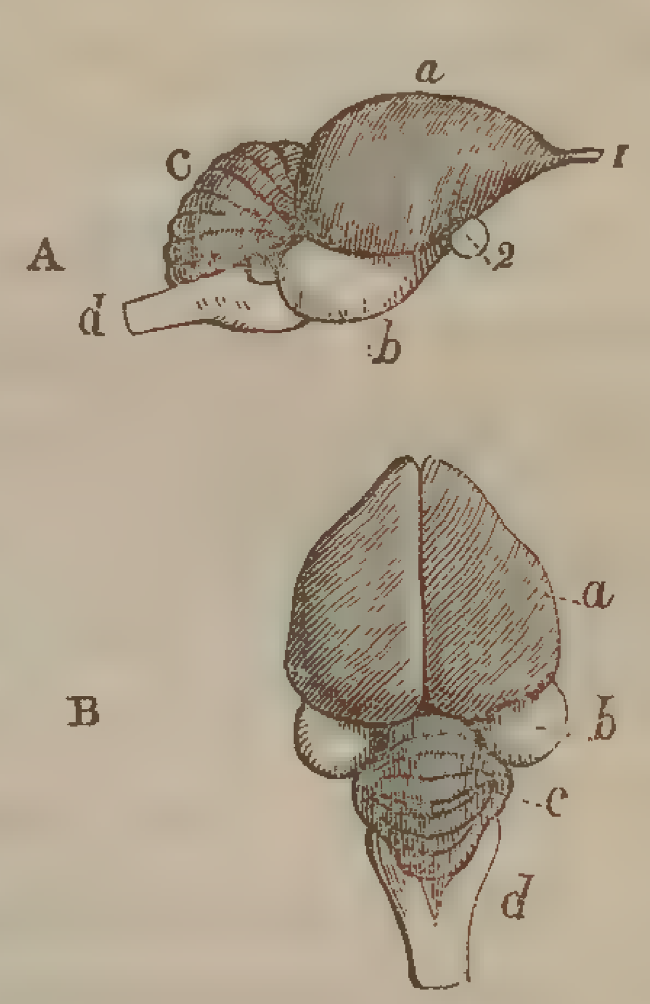
I. *Comparative anatomy of the brain of vertebrate animals.*

In no part of physiology can we derive greater aid from comparative anatomy than in the physiology of the brain. Corresponding with the developement of the intellectual faculties in the different classes, we meet with very great differences in the form of the brain, which are highly important in aiding us to determine the functions of the different parts of the organ. A knowledge of the comparative anatomy of the brain is also indispensable in the performance of experiments on animals, with a view to ascertain the properties of its individual parts. I

* Experimenta quædam de effectibus lesionum in partibus Encephali. Berol. 1826.

have on these accounts thought it necessary to preface the inquiry into the physiology of the organ by a review of its different forms in the vertebrate classes.

Fig. 50.*



A superficial comparison of the brain of the human subject with that of the higher animals is sufficient to enable us to recognise one important difference: it is, that the cerebral hemispheres, which in man overlap posteriorly not merely the corpora quadrigemina, but even the cerebellum, diminish more and more in their extent in that direction as we descend the scale, so as to leave those parts uncovered. In rodentia the cerebellum is already half exposed; in birds (fig. 50) the corpora quadrigemina have come to view; and they are more completely bare in reptiles. In proportion as the cerebral hemispheres diminish in size, the corpora quadrigemina or optic lobes enlarge; and although in reptiles (fig. 51) they are still considerably smaller than the cerebral lobes, in fishes the relative size of the parts is so altered that it is difficult to determine what each represents. The brain of fishes (fig. 52) consists merely of a series of double and single enlargements. The most posterior (*c*) is single, and lies upon the medulla oblongata, covering the fourth ventricle; it is the cerebellum. In front of this are two bodies (*b*), frequently the largest of all, and hollow in their interior; the optic nerves arise in greater part from them. More anteriorly are two solid bodies connected together in the middle line (*a*); and frequently in front of these, at the origin of the olfactory nerves, are two other enlargements not united together.

Fig. 51.†

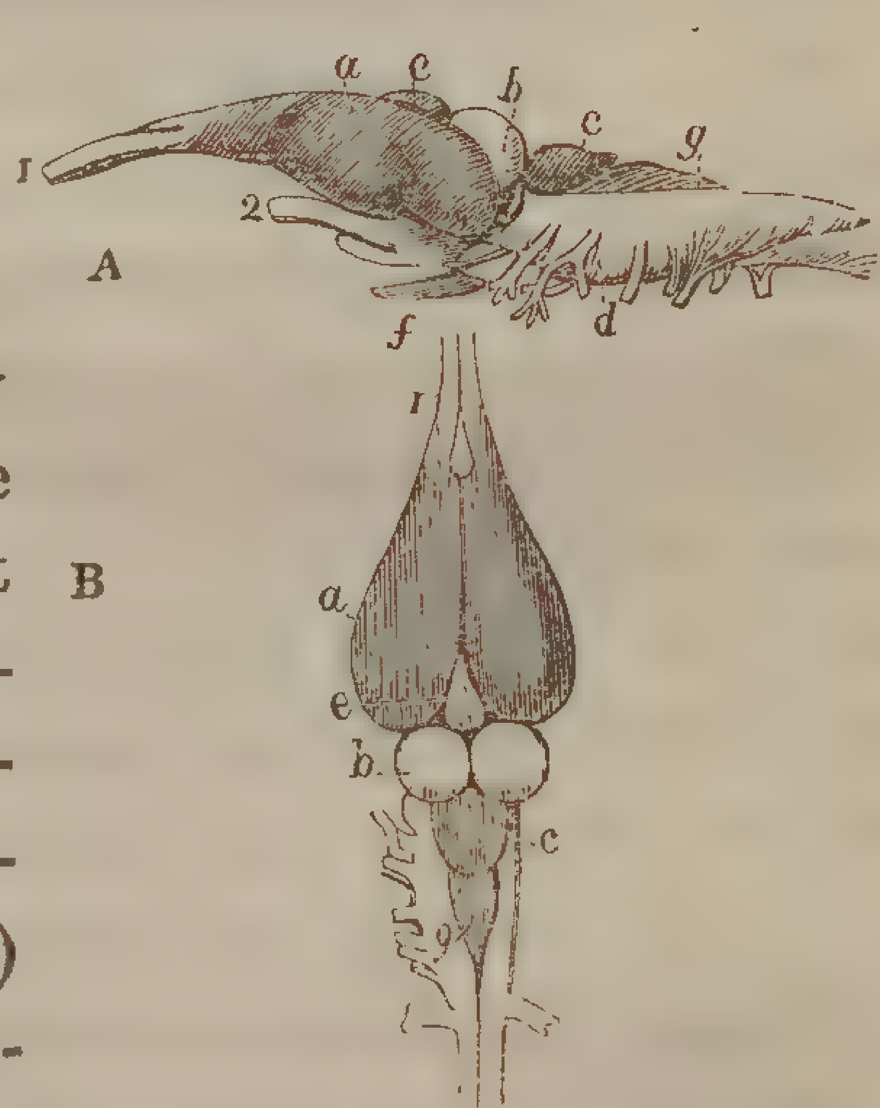


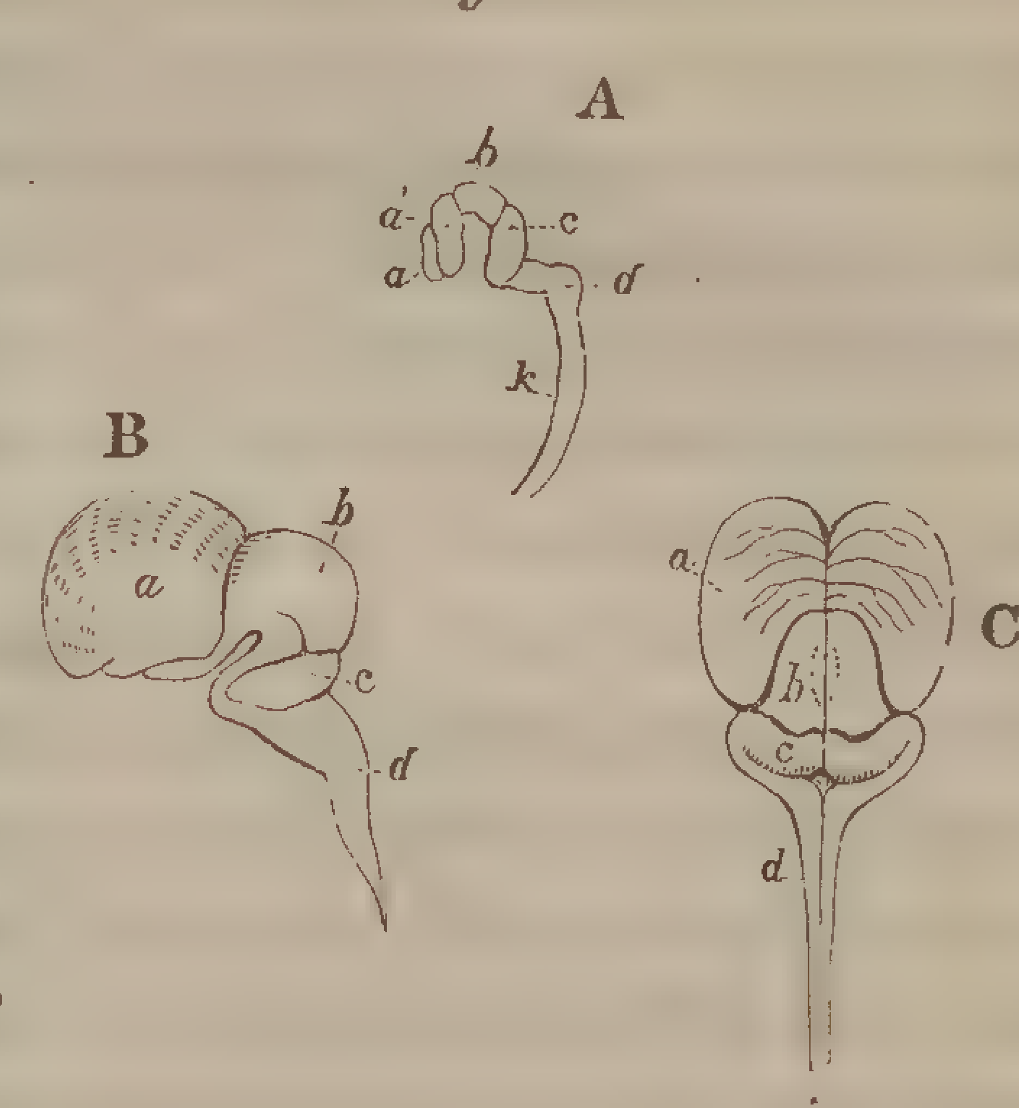
Fig. 52.‡

* Brain of a common fowl:—A, viewed from the side; B, from above. *a*, The cerebral hemispheres; *b*, the optic lobes or corpora quadrigemina; *c*, the cerebellum; *d*, the medulla oblongata. 1, The olfactory, 2, the optic nerve.

† Brain of a tortoise, after Bojanus, seen from the side A, and from above B. The cyphers, and the letters from *a* to *d* inclusive, refer to the same parts as in the former figure. *e*, The pineal gland; *f*, the pituitary gland; *g*, a vascular membrane covering the fourth ventricle.

‡ Brain of a perch, after Cuvier:—A, the lateral surface; B, the superior; C,

Fig. 53.*



The fœtal brain of the higher vertebrata (fig. 53), and that only, resembles in some measure the brain of the lower vertebrate animals; for in it the hemispheres are small, and do not overlap either the cerebellum or the corpora quadrigemina, (see fig. 53, B and C,) and at a very early period the latter bodies are not smaller than the cerebral lobes. At this time the brain of the higher animals presents a series of enlargements (fig. 53, A), like that of fishes: posteriorly the cerebellum (*c*), forming a single lobe in the middle line; in front of it the large vesicular corpora quadrigemina (*b*), not yet divided into an anterior and a posterior pair of elevations, the cavity in their interior being the ventriculus Sylvii, which afterwards is reduced to the aqueductus Sylvii; then the cerebral hemispheres (*a*), with the olfactory lobes at their anterior extremity in mammalia.†

The earliest condition of the brain of mammiferous animals is, however, not sufficiently well known to enable us to draw any useful deduction from a comparison of it with that of fishes. For this comparison we must take the brain of the embryo of the bird, which has been made the subject of investigation by Von Baer,‡ who describes it as presenting from behind forwards the following parts.

1. The cerebellum, a single body, covering the fourth ventricle on the dorsal surface of the medulla oblongata.

2. The vesicle of the corpora quadrigemina, from which the optic nerve principally arises; this has in its interior a cavity, the ventricle of Sylvius, which exists even in the adult bird when the corpora quadrigemina or optic lobes have become thrust to the lower surface of the brain and to a distance from each other.

3. The vesicle of the third ventricle. The third ventricle, bounded laterally by the optic thalami, and inferiorly by the infundibulum, is in the embryo still uncovered by the very small hemispheres. It is, however, originally not open superiorly; it is covered in by a vesicular

the inferior. The cyphers, and letters from *a* to *g* inclusive, refer to the same parts as in the two preceding figures. *h*, marks the enlargements of the medulla oblongata opposite the origin of the vagus; *i*, the lobi inferiores.

* Forms of the brain of the human fœtus, after Tiedemann:—A, at the seventh week; *a*, the cerebral hemisphere, a membrane-like body; *á*, the corpus striatum and optic thalamus; *b*, corpora quadrigemina; *c*, cerebellum; *d*, enlargement of the medulla spinalis (*k*). B and C, at the twelfth week; *a*, cerebrum; *b*, corpora quadrigemina; *c*, cerebellum; *d*, enlargement of the medulla spinalis.

† See Tiedemann's Anatomy of the Fœtal Brain.

‡ Burdach's Physiologie, ii.

roof, which afterwards becomes cleft anteriorly in the middle line, while its posterior part contracts to form what is afterwards called the pineal gland, the crura of this body being formed by the former expansion of the membranous roof. The vesicle of the third ventricle contains the optic thalami.

4. More anteriorly is the double vesicle of the hemispheres, in the cavity of which the corpora striata are seen forming the floor. This vesicle, which is at first smaller than that of the corpora quadrigemina or optic lobes, enlarges, and by degrees extends posteriorly over the vesicle of the third ventricle and its cleft. It is at first not open at its posterior border towards the vesicle of the third ventricle; in other words, the fissure of Sylvius, which in the adult opens under the lower posterior border of the hemispheres into the lateral ventricles, does not exist; so that, at a certain period, the only entrance into the vesicles of the hemispheres is through the fissure of the vesicle of the third ventricle, with which the cavities of the hemispheres communicate. But by the formation of a transverse fissure on each side, at the line of junction of the lower borders of the vesicles of the hemispheres with the vesicle of the third ventricle which they overhang, the fissure of Sylvius is produced, which is well known as leading, in the brain of the adult, under the posterior crura of the fornix into the lateral ventricles.

To this we will add a short description of the brain of fishes, (see fig. 52), commencing, like Cuvier,* with the cerebellum, since no doubt can exist as to its nature.

1. The cerebellum, (fig. 52, *c*,) a single body lying transversely above the medulla oblongata, and covering the fourth ventricle, which opens under it posteriorly, as in all animals.

2. The lobi optici (*b*), a pair of hollow lobes lying superiorly in front of the cerebellum, and connected with each other along a furrow in the middle line of their upper surface. They give origin to the optic nerves, and must not be confounded with the optic thalami. Their walls are formed of two layers of fibres, of which the exterior extends from behind and the outer side towards the lower and inner part of each lobe, while the interior layer radiates from below towards its outer and upper parts. At the bottom of their cavity (in the osseous fishes), lie two pairs of bodies, bounded externally by a grey mass which forms the centre of the internal radiation; in front of these bodies is the third ventricle, leading to the pituitary gland, and bounded anteriorly by the anterior commissure. The optic nerves arise from the exterior fibrous layer of the optic lobes. The passage (aqueduct), leading from the fourth to the third ventricle, opens in front of the grey bodies in the interior of the lobes. At the anterior extremity of the optic lobes,

* Hist. Nat. des Poissons, t. i.

between them and the lobi anteriores, is an opening in the middle line, which does not accord with the view of those who regard these lobes as corresponding to the cerebral hemispheres. The fourth nerve arises behind the optic lobes, and behind the grey bodies in their interior, in front of the cerebellum.

3. At the base of the brain, below the optic lobes and in front of the medulla oblongata, are two small bodies, the lobi inferiores (*i*), from which the optic nerves are stated by Cuvier to derive part of their fibres, although this is denied by M. Gottsche. In rare instances, they contain a cavity which communicates with the third ventricle.

4. In front of the optic lobes lie the lobi anteriores (*a*), ordinarily smaller in size, and of a grey colour; in sharks and rays, they are, however, of very large size. They are connected in the middle line by one or two commissures, and their surface sometimes presents convolutions. They are not hollow, except in sharks and rays. The olfactory nerves take their rise from them either directly, or with the intervention of the bodies called the lobi olfactorii, which, however, are not connected with each other by any commissure.

5. In some fishes, as the muræna, there is a body analogous to a pineal gland; when present, it lies in front of the optic lobes, and is connected by two crura to the posterior part of the base of the lobi anteriores.

6. In most fishes, there are enlargements (*h*) of the medulla oblongata, corresponding to the origin of the vagus; these are called lobi posteriores.

The frequent presence of an olfactory tubercle at the root of the olfactory nerves, and the origin of the optic nerves from the lobi optici, and of the vagi from the lobi posteriores, show clearly that the lobes of the brain in fishes are formed principally as central masses for the great nerves which arise from it; just as in the triglæ (flying fishes) the spinal cord presents a series of five pairs of enlargements at the points where the great nerves for the free appendages under their pectoral fins arise; and, as the cord has an enlargement opposite the origins of the nerves for the anterior and posterior extremities in all vertebrata.

The following are the different opinions held by comparative anatomists as to the nature of the different parts of the brain of fishes, as compared with that of higher animals.

1. Some, as Cuvier, regard the lobi optici of fishes as analogous to the cerebral hemispheres. They ground this opinion on the existence of the third ventricle in the floor of these lobes in the middle line, and on the presence of the anterior commissure in front of this ventricle. They compare the bodies in the cavity of the hollow lobi optici, and behind the third ventricle, to the corpora quadrigemina; and the lobi

anteriores they consider to be analogous to the olfactory lobes of reptiles, birds, and mammalia. M. Gottsche* also inclines to this view. The opinion of M. Cuvier is, however, rendered improbable by the position of the pineal gland in front of the optic lobes,—for if these lobes represent the cerebral hemispheres, the pineal gland must be placed anteriorly to the corpora quadrigemina,—and by the small size of the bodies in the cavities of the optic lobes, while the corpora quadrigemina of birds and reptiles are of very large size; though the commissures of the lobi anteriores of fishes constitute no argument against it, since the olfactory lobes of mammalia have a commissure.

2. Most anatomists, as Arsaky, Carus, Tiedemann, Serres, and Desmoulins, regard the optic lobes as analogous to the corpora quadrigemina of the higher animals, and the lobes in front of them as the cerebral hemispheres. This view is founded on the size of the corpora quadrigemina, and the presence of a cavity in them, in birds and amphibia; on their gradual increase of size in descending the scale of animals; on the partial origin of the optic nerves from the corpora quadrigemina in higher animals; and on the hollow structure and very considerable size of those bodies in the fœtus of mammalia, they being at a certain period of fœtal life larger than all the other parts of the brain. The position of the pineal gland in front of the optic lobes in fishes is also favourable to this view. The circumstances opposed to it are the solidity of the lobi anteriores (which are compared to the hemispheres) in all osseous fishes; the presence of bodies in the floor of the cavity of the optic lobes, which are not met with in the corpora quadrigemina of higher animals; and the existence of the third ventricle, with the anterior commissure in front of it, in the cavity of the optic lobes.

3. Treviranus regarded the optic lobes of birds as representing the posterior part of the cerebral hemispheres of mammalia together with the corpora quadrigemina, the corpora geniculata having become united with the latter bodies. This opinion rests principally on the circumstance of the posterior part of the optic thalami in birds projecting into the hollow optic lobes. According to this view, the optic lobes would result from the union of the posterior part of the hemispheres with the walls of the corpora quadrigemina, which in the fœtus are quite hollow.

4. The view which I take of the brain of fishes is, that the lobi optici correspond to the vesicle of the corpora quadrigemina, and that of the third ventricle seen in the embryo of the bird, which have coalesced. The correctness of this opinion is proved by the structure of the brain in the petromyzon (lamprey), in which, in place of the optic lobes, we have a lobe of the third ventricle, giving origin to the optic nerves, and

* See his excellent and accurate paper, über das Gehirn der Fische, in Müller's Archiv. 1835.

a vesicle of the corpora quadrigemina; while in all other fishes these parts form one common vesicle, in the floor of which the third ventricle is hollowed out. In the superior and anterior part of the lobe of the third ventricle in the brain of the petromyzon there is a fissure corresponding to that which is formed in the vesicle of the third ventricle in the brain of the embryo of the bird, and to that seen at the anterior part of the optic lobes of other fishes. This is a distinct proof that the optic lobes of fishes and of other animals are very different parts. The optic lobes of reptiles and birds correspond to the vesicles of the corpora quadrigemina in the brain of the embryo bird and mammal.* The lobi inferiores in the fishes' brain are likened by Desmoulins to the corpora mammillaria in mammalia; by Cuvier, to the optic lobes in birds, thrust still more to the base of the brain. The optic lobes of birds, however, although thrust asunder, and to the base of the brain, and although connected only by a transverse band, are evidently analogous to the great corpora quadrigemina of the fœtus of mammalia. (See fig. 53.)

If we compare the brain of reptiles and birds with that of mammalia, we find that, although in the former classes the fornix is present, the great commissure of the cerebrum, the proper corpus callosum, is not completely formed, except in mammalia. [It is an interesting fact, discovered by Mr. Owen,† that the marsupial mammalia, which in the fœtal state have no placental connection with the mother, resemble birds in the want of the corpus callosum.] The optic lobes of birds and reptiles, moreover, are hollow, while in the corpora quadrigemina of mammalia in the adult state the aqueduct of Sylvius, or iter à tertio ad quartum ventriculum, is the only cavity; and these bodies are not in the former animals divided into an anterior and posterior pair of eminences. The corpora albicantia are still wanting in birds and reptiles; and in them there is no pons Varolii externally visible, although the deep fibres which pass transversely between the bundles of the medulla oblongata in man and mammalia, and belong to the pons, are present. The lateral parts of the cerebellum are less developed than in mammalia.

If the brain of mammalia be compared with that of the human subject, there will still be found in the former a comparatively small developement of the cerebral hemispheres. In many animals there is no division of the brain into lobes; in the ruminantia, carnivora, pachydermata, and solidungula, we can distinguish two lobes to each hemisphere, which correspond to the anterior and the middle, rather than the posterior lobe of the human brain; and the absence of the posterior cornu of the lateral ventricle (except in apes, seals, and dolphins) is in favour of that view. There are scarcely any traces of convolutions, moreover, in many mammalia, as the rodentia, bats, mole, hedge-

* See Müller's Archiv. 1834, p. 62. † Philos. Transact. 1837.

hog, armadillos, and ant-eaters; and even in carnivora ruminantia, solidungula, pachydermata, and quadrumana, where alone they are distinct, they are still more simple than in the human brain.* The pons Varolii is visible externally, but is still narrow; hence the corpora pyramidalia of the medulla oblongata are left uncovered in a greater extent of their course. In many animals, also, fasciculi of transverse fibres surround the medulla oblongata, posterior to the proper pons, and separated from it.† In the medulla oblongata, the olivary bodies are not distinctly defined externally, nor their dentated figure internally; the transverse white lines on the floor of the fourth ventricle are usually wanting; and the cerebellum has a smaller number of lamellæ, and is inferior in its whole bulk to that of the human brain; while, on the contrary, the "flocks" (small lobules of the cerebellum seated on the very commencement of each peduncle) are, as in birds, more highly developed, and there are frequently depressions in the os petrosum to receive them. The olfactory lobes seen at the anterior extremity of the cerebral hemispheres in birds are still present in mammalia, and differ from the olfactory nerves of the human subject in containing a cavity which has a direct communication with the lateral ventricles of the cerebral hemispheres.

II. *Of the powers of the brain, and the mental faculties, generally.*

The brain undergoes a gradual increase of size from fishes up to man, in accordance with the developement of the intellectual faculties. Its proportion to the mass of the whole body is stated by Carus‡ to be,—

In the Burbot, (gadus lota)	as	1	to	720
Pike	,,	1	,,	1305
Silurus	,,	1	,,	1837
Salamander	,,	1	,,	380
Tortoise	,,	1	,,	2240
Pigeon	,,	1	,,	91
Eagle	,,	1	,,	160
Siskin, (fringilla spinus)	,,	1	,,	231
Rat	,,	1	,,	82
Sheep	,,	1	,,	351
Elephant	,,	1	,,	500
Gibbon	,,	1	,,	48
Simia Capucina	,,	1	,,	25

The maximum weight of a horse's brain is, according to Soemmering, 1 lb. 7 oz.; the minimum of an adult human brain, 2 lb. 5½ oz.; and nevertheless the nerves at the base of the brain are ten times thicker in the horse than in the human subject. The brain of a whale 75 feet in length, which is in the Museum at Berlin, weighed 5 lb. 5 oz. 1 dr. The weight of the human is, according to Soemmering, from 2 lb. 5½ oz. to

* Carus, Vergleich. Zootom. Bd. i. p. 75.—Anat. Comparée, t. i. p. 96.
† Treviranus, Vermischte Schriften, iii. 12. ‡ Anat. Comparée, t. i.

3 lb. 1 oz. 7 dr. When now we recollect that the spinal cord diminishes from mammalia downwards in a far less degree, (see page 794,) the inference appears manifest, that the developement of the intellectual faculties in the animal scale is dependent, not on the size of the medulla spinalis, but on that of the brain. The considerable variations in its proportional size in one and the same class show also that the size of the brain, as a whole, is not regulated by the mass of the body over which it presides, but that the motor apparatus proportioned to the mass of the muscles of the body is to be sought in the spinal cord. All parts of the encephalon, however, do not keep pace equally with the developement of the intellectual powers. It is in the cerebral hemispheres that the increase of size in the higher animals chiefly takes place. The cerebellum, also, becomes proportionally larger in animals higher in the scale, but in a far less marked degree. The corpora quadrigemina are actually smaller in proportion to the rest of the body; and the medulla oblongata, and its prolongations in the brain, are not proportionally larger in man than in any other animal. The nervous fibres from the whole trunk must in all animals equally pass through the medulla oblongata to reach the brain. Hence we perceive that the encephalon necessarily contains parts which have, in all animals, the same functions and importance for life; thus injury of the medulla oblongata is equally fatal to all, while injury to the cerebral hemispheres gives rise to a much slighter disturbance of the vital functions in reptiles than in animals endowed with higher mental powers.

We will not, however, at present enter into a consideration of the functions of the individual parts of the brain, independently of the intellectual faculties; but will first inquire into the relation which exists between the mind and the brain generally. Comparative anatomy alone suffices to show us that the source of the mental powers must be sought in the brain; and experiments on animals, as well as the history of lesions of the brain in comparison with those of other organs, confirm the suggestion. We have now, in the first place, to prove that the mental functions are performed in no other parts of the nervous system, or of the body generally, but in the brain alone.

With regard to the nerves, we learn, from the effects of lesions, that, when cut off from communication with the brain, they are withdrawn from the influence of the will, and impressions on them are no longer perceived; and in this respect the spinal cord resembles them (see page 797). On the other hand, the upper portion of a divided nerve, and the part of the spinal cord above the seat of the lesion, are still subject to the influence of the will, and the mind is rendered conscious of impressions made upon them. Thus the organ of the mind loses none of its powers by this division of the nerves and spinal cord; merely the number of the parts to which its influence extends is diminished,

just as by the amputation of his limbs a man loses none of his intellectual faculties.

Still less than the spinal cord can any other part of the body be the seat of the mental faculties. Limbs may be amputated, viscera affected with gangrene, and the mind still clear, as long as life continues. Delirium, certainly, sometimes attends inflammation of important viscera, but it may also be produced by inflammation of the skin of an extremity; and yet the whole limb, with the skin, may be removed without any loss to the mental powers. Violent inflammation of any part of the body produces a severe impression on the sensorium, and may cause delirium; but if the part become gangrenous or dead, this impression ceases, and thus occasionally a short time before death the mind regains its clearness. In this way it may be shown that none of the viscera of the abdomen can be the seat of the intellectual powers. The whole texture of the lungs, also, is sometimes seen to be destroyed by chronic disease without the mental faculties being impaired. So likewise, chronic disease of the heart does not interfere with the mental functions, except by causing disturbance of the cerebral circulation.

The effects of lesions of the brain are very different; every cause which disturbs its action slowly or suddenly affects at the same time the mind. Inflammation of the brain is never unattended with delirium, and at a later period with stupor; pressure on the cerebrum, whether produced by depressed bone, foreign bodies, serum, blood, or pus, always gives rise to delirium or stupor, according as there is or is not irritation with the pressure. The same causes, according to the seat of their action, frequently abolish the power of voluntary motion, or memory: and when the pressure is removed, the memory frequently returns; and it has been observed that the chain of thought was immediately resumed at the point where it was interrupted by the injury. Injury of the cerebral hemispheres in animals gives rise to stupor and loss of memory; and in most lunatics considerable structural changes have taken place in the brain, although in other cases, particularly when the affection is inherited, the changes that have affected the microscopic fibrous texture cannot be recognised with our imperfect means of investigation and defective knowledge. It has been said, as an objection to the brain being regarded as the seat of the mind, that very considerable disease has been found affecting an entire hemisphere without the mental faculties having suffered: experiments on animals show, however, that even sudden lesion of one hemisphere only does not immediately produce complete stupor, that this effect does not follow until both are removed; so that it would appear as if one hemisphere could aid the other, and even compensate for its inaction in the operations of the mind. Many distinguished writers, for

example Bichat and Nasse, although they admit that the brain is the seat of the higher intellectual faculties, still maintain that other organs also, as the abdominal and thoracic viscera, have a certain connection with the mental functions, and incline to the belief that the source of the passions may possibly be in these organs. They formed their opinion partly on the circumstance of the viscera of the chest and abdomen being affected during the prevalence of passions of the mind, and partly on their being frequently diseased in cases of insanity. The intestinal canal, liver, spleen, lungs, and heart are certainly frequently the seat of disease in lunatics, and occasionally even when no palpable change can be detected in the brain itself: and here the diseases of the abdominal or thoracic viscera may have been the exciting cause of the mental affection, but only in the same way as other causes might excite it by the impression communicated to the brain; there being in it some pre-existing disposition to morbid action, either hereditary or acquired. Hence in these patients, by removing the morbid change in the other viscera which have influenced the brain, the disposition in the latter organ to abnormal action may be reduced again to a latent state.

The relation in which the viscera stand to the mental emotions is, it must be confessed, still involved in much obscurity. The passions, by means of the change which takes place in the brain, affect the whole nervous system. The exciting passions give rise to spasmodic actions of certain muscles, particularly those of which the nerves belong to the respiratory system (including the facial nerve); hence the crying, sighing, sobbing, &c. with the spasmodic distortion of the features. In the depressing passions, as apprehension and terror, all the muscles of the body lose their tone, the supply of motor influence from the brain and spinal cord being arrested: the feet are not able to bear the body, the features hang motionless and without expression, and the loss of power may be so great as to cause momentary paralysis of the whole body, particularly of the sphincters. The motions of the heart are affected by both the exciting and depressing passions. The sensations of many parts are altered. The secretions, as those of the lachrymal gland and skin, are affected; the bile is not properly excreted, and permeates the coats of the blood-vessels so as to produce jaundice; the urine, lastly, becomes watery. The action of the capillaries is modified; hence the skin becomes red, or, in other cases, pallid. In short, the passions influence first the nerves engaged in the respiratory function; then, through the medium of the spinal cord, all the nerves of the trunk and extremities, as well those of animal life as the organic nerves. But I am not acquainted with a single fact which proves that in a healthy person a particular passion affects one organ more than another. It is usual to say that the heart is affected by joy, sorrow, and anxiety; but does not every exciting or depressing emotion alter its action? Does

not the heart stand in the same relation to the mental emotions as the lachrymal organs, which are affected by every emotion of the mind when it reaches a certain intensity? It is an old notion that the liver has a special relation to the passions of rage and vexation. Jaundice, with pain in the right side, or even inflammation of the liver, has certainly followed a paroxysm of these passions; but only in persons already suffering from affection of the liver, or having disposition to hepatic disease. Other persons, on the contrary, as a consequence of such emotions, have disturbance of the functions of the stomach; others again, an affection of the heart merely, this being in them the organ of which the action is most easily disturbed: and so it is with all the passions of the mind. In short, it is evident that the effects of the passions upon the different organs subject to the influence of the brain, in no way confirm the hypothesis of the passions or certain mental faculties having their seat in any other organ than the brain.

Although we are satisfied, upon grounds derived partly from comparative anatomy, and partly from physiology and pathology, that the seat of the mental operations is the brain and no other part,—that the nerves excite these operations and are the instruments for executing what the mind directs,—and that all the other parts of the body are subject to the influence of the nerves, still this amounts to nothing more than that the brain by its organisation is the instrument by which the mind operates and is active: we do not assert that the "essence" of the mind has its seat in the brain alone. It is possible for the mind to act, and receive impressions, by means of one organ of a determinate structure, and yet be present generally throughout the body.

The facts which we are about to mention prove conclusively that the mind, although its only seat of action is the brain, is itself, nevertheless, not confined to it. Two facts are sufficient. The one is that animals low in the scale, as planaria, polypi, and annelida, are divisible; and that polypi and annelida—for instance, the naides and nereides—propagate their species by spontaneous division (see page 19). It is evident from this fact that the vital principle is divisible; but since each portion of the divided animal evinces a separate will and special desires, we have a distinct proof that the mental principle of these lower animals, whether it be or be not identical with their vital principle, is also divisible. The second fact is, that the mental principle in the higher animals also, in man even, is, like the vital principle, in a certain limited sense divisible. The higher animals, and man, do not, it is true, generate new individuals, each endowed with a mind, by division of their own bodies into several portions; but they do this by the generation of semen in the male, and the ovum in the female. In whatever way the generation of the new individual be effected by the contact of the germ of the female

and the semen of the male, we know that in fishes, frogs, and salamanders, the mere contact of the semen and ovum brought together artificially, without any participation in the act by the male and female, is sufficient to produce a new individual. The germ and semen must therefore contain all that is necessary for the manifestation of the independent vital principle and the mental functions of the animal. In one or both of them the vital and the mental principle must exist as it were in a latent state; for otherwise these principles could not manifest themselves, as they are observed to do, during the after developement of the new individual. In the most perfect animals also, and even in man, we must suppose that the ovum and semen contain within themselves all the conditions necessary for the production of a new being endowed with life and mind; and consequently that one or both of them contain the vital principle, and the essence of the mind, in a latent state. The main question is not at all affected by the difference of the new individual being developed within the body of the mother, as in viviparous, or out of it, as in oviparous animals. From the foregoing facts and inferences we may perceive that the higher animals and man are so far divisible that a separated portion of their matter, namely, the generative fluids (germ and semen), is animated with the principles of life and mind; and, this being the case, that the mental principle cannot be confined to the brain, but must be contained, although in a latent condition, in parts which are far distant from the brain, and are separable from the rest of the body.

Whether the vital and mental principles be transmitted from the brain through the medium of the nerves to the semen or germ; whether the mind in a latent state be contained in the blood; whether in such a condition it exist in every part of the body, though free and active only in the brain, which is organised as its instrument and apparatus for the reception of impressions from other parts,—are all questions which it is impossible to answer, and the solution of which would not influence the result of our present inquiry. It is sufficient for our object to know that the semen and germ must contain not only the vital principle, but also the mind of the new being, in a latent state: thus that other parts of the body than the brain participate in being the seat of the mental principle, although this principle is manifested only in the brain, on account of the structure of that organ being adapted for its action upon the motor apparatus, and to the reception of the impressions communicated by the nerves. For consciousness, imagination, thought, volition, will, and passion, the brain is absolutely necessary; and although the principle for the production of ideas, thoughts, &c. is present in a latent state in the impregnated germ, yet the whole organisation of the brain must be created in this germ before the mental principle can become free, and the ideas, thoughts, and will

be manifested. In the anencephalous monster, of which the nutrition and life are maintained throughout the fœtal condition up to the time of birth, the organ generated in the living germ for the future manifestation of the mind has been destroyed (by hydrocephalus) at a period when it was not sufficiently developed to allow the exercise of the mental functions.

From the considerations and facts thus premised, we are now able to determine the question, whether lesions of the texture of the brain modify the mind itself; whether in mental affections the mind or its "essence" can itself be diseased, or whether merely the action of the mind by its instrument be altered. Since, as we have seen, the existence of the mental principle does not depend on an uninjured condition of the brain, and since it is certainly present, although in a latent state, in the germ separated from the parent animal, it is evident that a change in the structure of the brain cannot produce a change in the mental principle itself, but can only modify its actions. The action of the mind is dependent on the integrity of the fibrous structure and composition of the brain. The mode of mental action is always determined by the modification of structure and condition of the organ; but the mental "essence," its latent power, as far as it does not manifest itself, appears to be independent of all changes in the brain. According to this view, all inquiries as to the ultimate cause of affections of the mind, as regards their dependence on the brain or the mind itself, are useless; and the physician has to keep in view, as the first point in all abnormal conditions of the mental functions, merely the nature of the structural change by which the action is rendered abnormal or prevented. Two cases of congenital idiotcy have been reported to us, in which the cranium is so low that the representations given of them call to mind the state of the skull in hemicephalous monsters; but here the cranium is perfect. These idiots are the two sons of a widow named Sohn, living in the colony Kiwitsblott, a German mile from Bromberg; one is aged 17, the other 10 years. Both, enjoying excellent health, are at the same time so stupid that they do not remember their way back to their home if they leave it but a short distance; and cannot unbutton their breeches, although they have full powers of motion and volition in all parts of their body: they manifest their volition only in eating and drinking, and in destroying every thing which comes into their hands; they are, however, tractable, and harmless in disposition. Even in these remarkable cases we cannot imagine that any congenital disease of the mind itself existed—any original defect of the mental principle; in the latent state of this principle in the germ, there was, without doubt, all present which was necessary for the highest perfection; but, on account of the imperfect formation of the brain, the developement of the higher mental faculties became impossible. In the same way, in a healthy man, a sud-

den change in the condition of the brain modifies the manifestation of the mental principle, or even renders it latent; but, if the pressure which impeded the action of the brain be removed, the functions of the mind are frequently restored in their entire integrity.

Since the action of any part always induces a change in the organic matter which composes it, (see page 52,) it necessarily follows that immoderate exertion of the mind, a continued direction of it to one object consequent on external circumstances or great mental excitement, must react on the organisation of the instrument of the mental operations; and, although the removal of these causes may be very important in the eyes of the physician, yet the state of the organ itself is the proper object of his treatment; and the wrong direction of the thoughts is not the essence of the mental disease, but can merely be one among its numerous exciting causes.*

The question, whether the vital principle by which the whole organisation of the germ, and even the formation of the organ of the mind, are effected, be essentially different from the mental principle or "essence," or whether the operation of the mind is merely a mode of action of the vital principle, is not capable of solution by physiological facts. We know that the vital principle may continue to act without any mental power being manifested; for instance, in monsters devoid of brain and spinal cord. But we cannot thence conclude that the mental is essentially distinct from the vital principle; for we have already seen that the former may exist in a latent state in a living body, separately from the brain. It would be equally incorrect to infer, from the fact just stated, that the mental principle is only a mode of action of the vital force; it only proves what indeed the formation of the embryo before the developement of faculties sufficiently shows,—namely, that the action of the mind is not necessary to the operations of the vital principle,—while it is equally certain that the action of the mind cannot go on unless the vital principle be also present; for the original production and continued maintenance of the organisation of the brain necessary for the manifestation of the mind, are due to the vital principle.

In favour of the view, that the mind is merely a particular manifestation of animal life, may be urged the fact, that it is not confined to one class of animals, or to man, but is possessed even by the lowest creatures; for mind cannot be denied to any animal which is conscious of internal images, independent even of external impressions on the senses,—has thoughts and desires, forms ideas concerning the objects of these desires, and the mode of satisfying of them, and by ideas and desires is impelled to voluntary actions. In this sense mental phenomena are presented even by the lowest animals; the passions are manifested principally only in the

*[Some German writers, as for example Heinroth, have gone so far as to regard all insanity as a wrong action of the soul, and to speak of the insane as sinners.]

higher animals. On the other hand, for the opinion that the mental is independent of the vital principle, it may be argued that one whole division of organised living beings, namely, plants, are destitute of all mental manifestations. This objection may, however, be met by the supposition, that here the vital principle is in a latent state in relation to its mental actions; and when a hypothesis rests merely on its explaining a great number of facts, its force is neutralised, if another, which affords an equally good explanation of them, b opposed to it.

The actions of both principles—the mind and life—agree in manifesting reason; but the reason of the mind is merely the consciousness or perception of what is rational; it has no creative influence on the organisation, on the organic matter: the reason of the vital principle, on the contrary, is manifested in the production of a well-adapted organisation in the living matter. The reason manifested in the organisation of the simplest being is, perhaps, of a higher character than the mind of an animal, or of man, can possibly conceive. All the problems of physics yield to this creating power. To the power which formed the eye and ear the physics of sight and hearing have no problems unsolved. It is the cause of instinct—that is to say, it is owing to this power that in the sensorium of an animal dreams arise which impel it to actions adapted to its condition—actions necessary to its existence, and evidencing reason, although the mind of the creature has not the slightest perception of the reasoning process on which these actions depend.

If there be any true ground for the view that the mind is merely a mode of manifestation of animal life, it is that both the one and the other may be the result of the action of "reason," that the production of the organisation of the simplest animal in the developement of the germ presents evidences of the highest rational power, and that the reason manifested in this creative action far excels all the mental powers of animals. Stahl attributed all the actions of the animal body to the soul or mind, because they evidence adaptation. This soul,—though the mental functions, in the more confined sense, be dependent on it, and the product of its operations,—is, in the sense in which Stahl conceived it, something of a very different and higher nature than what we usually understand by the mind. It is easy to perceive that Stahl's theory was founded on the observation of the rational operations of the vital principle, and that he regarded the mind as a mere manifestation of that primum movens. But even though this view be correct, which cannot be proved empyrically, yet it must be remembered that the mental functions embrace but a small part of the operations of this power which is the primary cause of the existence of the being, and which provides in its organisation and in its instinctive impulses against all that may happen to it in its final communication with the external world.

Another question agitated is, whether the mind be a property of mat-

ter, or an independent power or principle; whether it be a principle superadded or united to the body; or whether it be nothing more than the expression, as it were, of a certain condition—of a certain combination of matter. Motion or action is, perhaps, a primitive inherent condition of matter, since even the state of repose of inorganic masses is dependent on the reciprocal attraction of their particles. If, then, there be no body which does not possess an energy, force, or action; may not the mind itself be the property resulting from a certain condition or combination of matter in living beings? What is the cause of the absence of all signs of mental action in the body after death? Is it that the matter has lost its peculiar condition or composition,—the united action and attraction of its vivified atoms; and that these, their condition being altered, henceforth manifest other properties? or is it that the mental principle has really separated from the body?

The phenomena of the mind, whatever be the nature of its essence, are without doubt closely and necessarily connected with the organisation of the brain. Unless the complicated fibrous structure of the brain be in an unimpaired state, mind is not manifested in the body; but still it may exist in it in a latent condition, just as in the generative fluids from which the new creature endowed with mind is developed. But here again it may be asked, is this latent condition of the mind only the state of rest of a power inherent in a certain combination of matter? or can the mental principle, itself independent of all matter, be at one time superadded to, at another separated from it? Do the atoms (according to the doctrine of materialism, the only source of action,) return, when the matter animated with the latent state of life is decomposed, into the general mass of inanimate matter, to become the source of new life when again brought together in a certain combination? or are the principles of life and the mind in their latent state independent of the decomposition of the atoms? is their "essence" immaterial, and not the property of atoms of matter, or of a certain combination of atoms? Although physiology cannot afford a solution of these problems, still there are facts which have a certain relation to them. There are, namely, forces in nature,—imponderable substances, which, although not independent of matter, nevertheless pass from one body to another without the matter of either of these undergoing any apparent changes; such are light, electricity, and magnetism. The existence of these principles, their manifestation in bodies, and their passage from one body to another, is an evident proof that the doctrine of materialism, which admits the existence of no principles but as properties of material atoms, is without foundation; and without, in the remotest degree, wishing to compare the vital and mental principles with the imponderable agencies just mentioned, we must express our conviction that there is nothing in the facts of natural science which argues against the possibility of the

existence of an immaterial principle independent of matter, though its powers be manifested in organic bodies in matter.

We must here recur to another problem, which has been already touched upon at page 39. It refers to the cause of the constant destruction and reproduction of individual beings endowed with life and mind. The vital principle not only increases in intensity during the growth of organised beings, but it is also multiplied by division and generation. From one organised being many others are produced endowed with equal vital and productive power; from these again, many more; while the vital principle of the individuals seems, at death, to perish or become latent. In this multiplication of living beings, the vital force is not simply transmitted from one to the other; for the parent being remains, even after manifold propagation, still capable of producing new individuals, until it at last perishes. In the case of the mental principle, the same law prevails. The parent loses none of its intellectual power, even by the repeated generation of new beings endowed with mind; but at length, death occurring, the mind of the parent is rendered latent. How can we explain this infinite multiplication of the vital principle and mind, which attends the constant production of new individuals, while the parent beings retain their life and mental power unimpaired? Two hypotheses are offered, but neither is capable of proof. According to the first, the principle of life and the mental principle are contained in a latent state in all matters which afford nourishment to animals, and are merely rendered manifest by the organisation of living beings. This is the solution adopted by the Pantheists; who doubt the immortality of the individual beings, admitting merely the existence of one immortal universal spirit. The second mode of solving the problem is, by supposing, not that the vital principle and the mind are latent in all matters which living beings can appropriate for their nourishment; but that the vital principle exists only in living beings, and that the mental principle is united with them, superadded to their matter, only during their life. According to this view, the multiplication of individuals endowed with mind can be explained only on the assumption that the mental principle, if it be multiplied by generation *ad infinitum*, is a force which division can never diminish in quantity or intensity. A supposition which, for our powers of reasoning, is incomprehensible; but to which every one is impelled who contends against the doctrine of pantheism, and embraces the belief in the immortality not of the mental principle generally, but of the individual reasoning beings,—a belief which is innate in us, and which carries us over the chasm which no science can fill up.

Here the mind is considered only in its most general relations to the brain: its special physiology will be discussed in the sixth book.

III. *Of the medulla oblongata.*

The brain and spinal cord react on each other through the medium of the medulla oblongata; hence the importance to physiologists of a knowledge of the course of the different columns or bundles of fibres of this part. Burdach* has thrown more light on this subject than any other anatomist. The following parts are now distinguished as composing the medulla oblongata.

1. The corpora pyramidalia, formed, according to Burdach, of fundamental and decussating fibres. The former lie at the anterior surface of the grey central column, and form the posterior wall of the anterior fissure of the spinal cord; but as they ascend in the neck, between the space of $3\frac{1}{2}$ to $1\frac{1}{2}$ inches below the pons, they pass obliquely forwards, so as first to form the lateral boundaries of the anterior fissure, and at last to appear at the two sides of this fissure on the anterior surface of the spinal cord and at the inner side of the anterior columns. The decussating fibres are a branch of the lateral columns of the spinal cord; they run behind the olivary body, ascend, passing obliquely inwards and forwards, and with the former set of fibres appear at the surface of the cord one inch below the pons Varolii, at the side of the anterior fissure. The decussating fibres alone pass from one side of the fissure to the other to join the fundamental fibres of the opposite pyramid.† The fibres of the corpora pyramidalia pass between the transverse fasciculi of the pons to reach the crura cerebri.

2. Fasciculi of fibres which run at the inner and outer side of the olivary bodies, and which are not seen on the surface of the medulla oblongata. (Fasciculi siliquæ. Burdach.) The anterior of these fasciculi is formed of the fibres which bounded the anterior fissure of the spinal cord, and which have been thrust outwards by the corpora pyramidalia rising to the surface. The external fasciculus is the outer portion of the anterior column of the spinal cord lying at the inner side of the anterior roots of the nerves. Both these fasciculi, which sheath the olivary bodies, are in contact with each other till they reach these bodies. The internal fasciculus passes with the pyramids through the pons into the crura cerebri: The external is continued upwards and inwards, around the upper portion of the processus cerebelli ad testes, to the base of the corpora quadrigemina.

3. The olivary body is formed by the expansion of the anterior grey column of the cord. At this point the grey column forms a plicated vesicle of grey matter, filled internally as well as invested externally with white fibrous substance. This it is which produces in a section of the corpus olivare, the appearance called corpus dentatum.

4. The lateral column of the spinal cord gives off from its inner side

* In his excellent work, Vom Bau und Leben des Gehirns. † Burdach, ib. ii. 31.

at the commencement of the medulla oblongata the decussating fibres of the anterior pyramids; the remaining portion is continued over the olivary body into the processus cerebelli ad medullam oblongatam, (corpus restiforme) and partially also into the external part of the fourth ventricle.*

5. The fasciculus cuneatus is the continuation of the medullary fibres which cover the posterior grey columns of the spinal cord, and which, lying at the upper side of the lateral column, form with it the process from the medulla oblongata to the cerebellum; its internal fibres run at the outer part of the walls of the fourth ventricle towards the cerebrum. [According to Mr. Solly, some fibres of the anterior columns also of the spinal cord contribute to form the corpus restiforme, or processus cerebelli ad medullam oblongatam, interlacing in it with those derived from the lateral columns.]

6. At the inner and posterior surface of the corpus restiforme lies a delicate fasciculus of fibres (fasciculus gracilis), the inner side of which forms the lateral wall of the posterior fissure, and is, in part, in close contact with the corresponding surface of the fasciculus of the opposite side. At the apex of the fourth ventricle, this fasciculus becomes swollen into a club-shaped body (clava).†

7. The "round fasciculi" (fasciculi teretes) are rendered visible by the divergence of those last described; as lateral walls of the canal of the spinal cord they lie between the corpora restiformia in the floor of the fourth ventricle, and pass forwards, separated by the median fissure, to form the anterior and inferior boundary of the aqueduct of Sylvius.‡

Properties of the medulla oblongata.—It has the general properties of the medulla spinalis. It has, namely, the property of reflection, indeed in a higher degree than any other part of the nervous system; the nerves which arise from it are more prone than any other part of the nervous system to reflex action; it belongs to the motor apparatus, and no part has so great an influence on the production of motions, for irritation of it excites convulsions of the whole trunk, and by lesion of it the whole trunk is paralysed. But the properties which especially distinguish the medulla oblongata are the following:

1. *It is the source of all respiratory movements*, as has been shown at page 348; of the natural movements of respiration, and of the spasmodic affection of the respiratory muscles excited by irritation of the mucous membranes (see page 351). The passions, in exciting the respiratory

* Burdach, ibid. p. 35. † Burdach, loc. cit. p. 37.

‡ For a full detail of the course of the fibres in the brain I refer to Burdach's work, and to the "Icones" of Langenbeck; for an account of the later investigations into the structure of the brain, Weber's edition of Hildebrandt's Anatomie, M. D'Alton's article in the 11th volume of the Encycl. Wörterb. der Medicin. Wissensch. [and Mr. Solly's work on the Brain] may be consulted.

nerves (the facial included), act through the medium of the medulla oblongata. The same movements, as laughing, crying, and yawning, are also frequently excited by the influence of the sensorium occupied by certain ideas, on the medulla oblongata. The central part of the nervous system seems always to have in the state of fatigue a disposition to the production of yawning, which is immediately excited if the idea enters our mind from seeing others yawn.

2. *It is the seat of volition.*—The experiments of M. Flourens show that animals in which the cerebral hemispheres have been removed, though in a state of stupor, are still capable of executing voluntary movements; they have still this power of volition after the removal of the cerebellum also, but by this last mutilation their movements are deprived of force and co-ordination.*

3. *The medulla oblongata is the seat of the faculty of sensation.*—This is not merely shown by the anatomical fact that all the cerebral nerves, with the exception of the first and second, are connected with it, or with its prolongations in the brain; it is proved also by the history of experiments on the different parts of the encephalon. From the researches of Magendie and Desmoulins it results that the removal of the cerebral hemispheres and the cerebellum does not deprive an animal of the power of sensation. The central organs of the senses of sight and smell are lost with the cerebral hemispheres, and blindness ensues; but the consciousness of sensations does not appear to be the function of the cerebrum. Flourens concluded from his experiments that the cerebral hemispheres are alone the central organ of sensations. But this is not a legitimate inference from his highly interesting observations, which, as Cuvier has remarked (in his Report to the Academy on the Memoir of M. Flourens), prove directly the contrary of this. An animal in which the cerebral hemispheres have been removed is in a state of stupor; but presents, nevertheless, manifest signs of sensibility, and not merely of the reflection of impressions. It no longer performs any voluntary movements; but, when struck, it has all the manner of an animal waking from sleep. In whatever position it be placed, it resumes the equilibrium. If laid upon the back, it rises again; if pushed, it walks. If it be a bird, and we throw it up into the air, it flies; if it be a frog, it leaps when touched. The animal has, doubtless, lost its memory—it no longer reasons; but nevertheless it feels, and the sensations excite in it movements which are different from the phenomena of mere nervous reflection. Cuvier very aptly compares animals in this condition to a sleeping man; he also seeks an easy position; he feels.†

* Müller's Archiv. 1834, p. 168.

† See Cuvier's Rapport, &c. in M. Flourens' work, Sur les proprietés et les fonctions du Systême Nerveux. Paris, 1824, p. 77.

Sensation itself must be distinguished from "attention," (the direction of the mind to sensations,) and from the faculty of forming ideas from sensations. Attention appears to be a function of the cerebral hemispheres; by their removal the animal is rendered stupid, though sensation remains. Among a certain number of simultaneous sensations we are able to direct our attention to a single one, so as to perceive it, not only more distinctly than the rest, but definedly and in its whole intensity; this sensation excites in us ideas, while those to which attention was not directed are perceived, but only indistinctly. While, therefore, the medulla oblongata is susceptible of obscure sensations, the distinct perception of sensations is dependent on parts of higher function, which are lost when the cerebral hemispheres are removed.

Some have believed that the medulla oblongata is the central organ for all sensations. This appears to me to be an error, if by medulla oblongata be meant only the superior enlarged portion of the spinal cord, and not also its prolongations into the cerebrum. The medulla oblongata, in the restricted sense, is certainly the receptacle for all the sensations of touch; these sensations are felt even after the cerebrum is removed, but indistinctly,—the mind is not directed to them. On the other hand, for the senses of sight and smell there are central organs which lie in the cerebral hemispheres: blindness, for example, is produced by mutilation of the anterior pair of the corpora quadrigemina, the thalamus opticus, or of the deep-seated parts of the hemispheres generally. It appears, therefore, that the central organs of the different senses are independent of each other; if they do in part belong to the prolongations of the fasciculi of the medulla oblongata, still it appears that their actions may be isolated, a reciprocal action of each with the hemispheres of the brain being necessary for a distinct perception of the sensation of which it is the seat. This is probable, but many facts are wanting to prove it. It appears to be certain that, after the removal of the central organ of vision, the impressions on the nerves of common sensation are still felt; but it is not known whether, after the destruction of the medulla oblongata, impressions on the other senses can still be perceived. Injury to the medulla oblongata puts a stop to respiration, and thus reduces life to such a low ebb that it is impossible to institute experiments as to the persistence of the sensations of sight, smell, &c. It is, however, most probable that the actions of the different organs of the senses are ultimately communicated to the cerebral hemispheres, and not to the medulla oblongata, and that it is in them that the separate sensations are converted into ideas.

With reference to the sense of hearing, it is usually supposed that its central organ is the floor of the fourth ventricle, since the fibres of the auditory nerve have their origin there. Flourens, on the contrary, main-

tains that, after the removal of the cerebral hemispheres (which birds survive many months), hearing is lost. But whether the sense of hearing be dependent on a state of integrity of the floor of the fourth ventricle or not, the transverse white fibres which are seen on it appear to have by no means the important influence on the sense of hearing which is often attributed to them; they are by no means constantly connected with the auditory nerve, and sometimes pass distinctly over the superior root of the nerve into the crus cerebri. In the Museum at Berlin there is the brain of a young female, who, in consequence of a fall upon the neck and occiput, was gradually attacked by paralysis of the whole body; and here, on the floor of the fourth ventricle, and upon these transverse white fibres, an effusion of lymph has taken place, although the sense of hearing had not suffered.*

IV. *Of the corpora quadrigemina.*

The corpora quadrigemina of mammalia, and the lobi optici of birds, reptiles, amphibia, and fishes, belong, with the optic thalami of the higher animals, to the central apparatus of the sense of vision. If in a pigeon one of the lobi optici be removed, or in a mammiferous animal one half of the corpora quadrigemina, blindness of the eye of the opposite side is produced, according to Flourens; but the mobility of the iris is preserved for a long time. (M. Magendie did not find this result in mammalia). According to MM. Magendie and Desmoulins, the animals turn frequently upon their own axis, towards that side on which the removal of the optic lobe has been effected. This movement, which was observed even in frogs, appears to be the result of vertigo. Flourens covered one eye in healthy pigeons, and they turned round in a similar way; but not so briskly, and for a shorter time. The removal of the optic lobe is always attended by convulsions of the opposite side of the body, of which the muscular power is afterwards much impaired. It is a remarkable fact that, while injury to one of the optic lobes always destroys the sight of the opposite eye, yet the contractility of the iris under the influence of light is not lost if the mutilation be only superficial; a complete removal of the optic lobe paralysing the iris as well as the sense of sight. Flourens explains this on the supposition that a partial removal of the optic lobes does not abolish the excitability of the optic nerves, because it does not destroy all their roots. The motion of the iris is certainly dependent on the excitation of the optic nerves by light; for Flourens found that irritation of these nerves caused the iris to contract, and division of them paralysed its motions. The explanation given by Flourens is correct; but, when the optic lobe is partially removed on one side only, the action of light on the retina which is not paralysed will explain the contraction of the iris of the

* See Fischer, de rariore Encephalitidis casu. Berol. 1834.

blinded eye [see page 712, and the note ‡ at page 721]. The researches of M. Hertwig* have afforded a confirmation of the experiments of Flourens in almost every particular. The results which M. Hertwig obtained are: 1. that the partial mutilation of one half of the corpora quadrigemina or optic lobes in mammalia and birds produces partial loss of power and blindness of the opposite side of the body,—that vision, however, is regained after a certain time; 2. that this partial lesion does not abolish the motions of the iris,—on the contrary, that these motions sometimes continue; 3. that by removing a larger portion of the optic lobe, or completely extirpating it, vision, as well as the contractile power of the iris, is completely destroyed; 4. that mutilation of the optic lobe has nearly the same effect on the eye as injury to the optic nerve; 5. that the muscular weakness of the opposite side of the body, produced by the mutilation of one optic lobe, is only temporary; 6. that the infliction of this injury on one side of the body causes the animal to move round on its axis, as if giddy; 7. that no other effect than those mentioned follow the mutilation of the corpora quadrigemina,—thus, for example, that no disturbance of memory or consciousness is produced.

The only point in which the observations of this experimentor differ from those of M. Flourens, has reference to the convulsions produced by injury to the optic lobes, which, in M. Hertwig's experiments, never ensued. The opposite result obtained by M. Flourens was perhaps due to his incision being carried too deeply.

V. *Of the cerebellum.*

The functions of the cerebellum have been made the subject of interesting experiments by Rolando, Flourens, Magendie, Schoeps, and Hertwig.

M. Rolando constantly observed that the diminution of the movements was in a direct ratio with the lesion of the cerebellum; that stupor was never produced, nor the sensibility of any part of the body impaired; but that the power of the muscular movements was lost. The animals keep their eyes open, and regard surrounding objects, but in vain endeavour to execute any of the movements necessary for locomotion. An animal in which one side of the cerebellum has been removed, falls upon the same side, not being able to support itself upon the leg of that side. These results induced Rolando to adopt a supposition quite incapable of proof, namely, that the cerebellum is the organ destined for the generation of the nervous principle, which he compared with electricity; and that the alternate layers of white and grey substance of the cerebellum act, as Reil also imagined, in the way of a galvanic pile.

The experiments of M. Flourens† are clearer and more decisive in their

* Exp. de effect. læsion. in partibus Encephali. Berol. 1826.

† Loc. citat. pp. 18 and 36.

results. He found that the animals evinced no signs of sensibility in the cerebellum while it was being removed. He extirpated the cerebellum in birds by successive layers; feebleness and want of harmony of the movements were the consequence. When he had reached the middle layers, the animals became restless without being convulsed; their movements were violent and irregular, but their sight and hearing were perfect. By the time that the last portion of the organ was cut away, the animals had entirely lost the powers of springing, flying, walking, standing, and preserving their equilibrium. When an animal in this state was laid upon the back, it could not recover its former posture; but it fluttered its wings, and did not lie in a state of stupor; it saw the blow which threatened it, and endeavoured to avoid it. Volition, sensation, and memory, therefore, were not lost, but merely the faculty of combining the actions of the muscles in groups; and the endeavours of the animal to maintain its equilibrium were like those of a drunken man. The experiments afforded the same results when repeated on all classes of animals, and from them Flourens infers that the cerebellum belongs neither to the sensitive nor to the intellectual apparatus; and that it is not the source of the voluntary movements, although it belongs to the motor apparatus: the infliction of wounds in it does not, however, he says, excite convulsions, as when other motor apparatus, such as the spinal cord and medulla oblongata, are wounded;—but the removal of it destroys the force of the movements, and the faculty of combining them for the purposes of locomotion,—the faculty of the co-ordination of the movements. If this view be correct, the cerebellum must contain a certain mechanism adapted to the excitement of the combined action of muscles, so that every disturbance of its structure must destroy the harmony between this central organ of combined motions, and the groups of muscles with their nerves. It is also to be remarked, that injury to the cerebellum always produces its effects on the opposite side of the body.

The observations of Flourens relative to the insensibility of the cerebellum itself, and the influence of injury of it on the combined movements, leaving the senses and all other functions of the body unaffected, are confirmed by Hertwig, who remarked, however, that if the mutilation of the cerebellum have been partial only, its function is restored. Hertwig also found that removal of one side of the cerebellum affected the movements of the opposite side of the body.

M. Magendie states that hedgehogs and guinea-pigs, in which he had extirpated both cerebrum and cerebellum, rubbed their nose with their paws when vinegar was held to it. He asserts also that, when the wound is inflicted on the cerebellum, the animal makes an effort to advance, but is compelled by an inward force to retrograde. Injury to the crus cerebelli or processus ad pontem, and of the pons itself, upon one side,

always caused the animals to roll over towards the same side. The same effect is produced by every vertical section which involves the medullary mass lying over the fourth ventricle, but it is seen in the most marked degree from injury of the crus. Sometimes, M. Magendie says, the animals made sixty revolutions in a minute, and he has seen this movement continued for a week without cessation. These are not convulsive movements, but are voluntarily performed, as if under the influence of an internal impelling force, or as if the animal were attacked with vertigo. Division of the second crus cerebelli is stated by M. Magendie to restore the equilibrium. Hertwig also observed in a dog in which the pons Varolii was wounded on the right side, that similar revolutions of the body towards the same side were performed, and one eye was turned upwards while the other was turned downwards. Superficial wounds of the pons were, in Hertwig's experiments, attended with moderate pain; he believes each half of the pons to influence the opposite half of the body. No convulsions followed injury to it.

The restiform bodies belong to the medulla oblongata; injury inflicted on one of them in a goat was found by Rolando* to produce convulsions, with curving of the body of the animal to the injured side. Wound of the processus cerebelli ad testes was observed by the same author to cause convulsions which affected in the greatest degree the extremities of the opposite side of the body; the animal, a rabbit, fell upon the side on which the lesion was inflicted each time that it made a spring.

Gall regards the cerebellum as the organ of the sexual impulse. The grounds on which this view is founded are not conclusive. Burdach† has collected the facts which bear upon this question. He has calculated that affection of the sexual passion is observed once in every seventeen cases of lesion of the cerebellum, and once in three hundred and thirty-two cases of lesions of the cerebrum. In apoplectic cases attended with erection of the penis, there has been found effusion of blood in the cerebellum.‡ Dunglison observed priapism in a case of inflammation of the cerebellum with serous effusion. Destruction of the spinal cord in animals also gives rise occasionally to erection of the penis. The observations of Heusinger,§ that, in two birds which died suddenly, there was a turgid state of the testicles and effusion of blood in the cerebellum, cannot be adduced as proof of the correctness of Gall's hypothesis; and all the other cases of simultaneous disease of the cerebellum and affection of the sexual functions do not really prove much. The coincidence of disease of the spinal cord with affection of the genital organs is much more frequent.

The developement of the cerebellum in the scale of animals presents no relation with the energy of the sexual impulse. In the amphibia (as

* Saggio, &c. ed. 3. p. 128.
† Op. cit. iii. p. 423.
‡ Serres, in Magendie's Journ. iii. p. 114.
§ Meckel's Archiv. vi. 551.

frogs and toads) this organ is extremely small, constituting a mere band lying over the fourth ventricle, and nevertheless the sexual instinct of these animals has become proverbial, although they have no erectile organ.

A preparation in the anatomical museum at Bonn* is unfavourable to Gall's opinion. It is the cerebellum of a man in whom half the organ was found atrophied. Death had been caused by an inflammatory disease. But the sexual passion had been rather strong than weak; the man was married, and father of several children. The facts detailed by Cruveilhier† are, however, the most remarkable. In one case, an individual twenty-one years of age, two large tuberculous masses were found in the left hemisphere of the cerebellum, although there had been no paralytic symptoms, no pains in the head, and no positively unnatural phenomena in the genital organs. Since the subject of this disease is said to have had no desire for sexual pleasures, the case might be regarded as a proof of the correctness of Gall's hypothesis. In the second case, however, there was coincidence of complete want of the cerebellum with tendency to masturbation; it occurred in a girl of eleven years. When seven years old, she presented great weakness of the extremities, want of intelligence, and indistinct articulation. At the eleventh year, when she was more closely observed, the feebleness of the extremities was so great that she could scarcely move her legs, although their sensibility was perfect. She could move her arms. Her intellect was very dull. After death, which was caused by an inflammatory disease, the inferior occipital fossæ were found filled with serum. In place of the cerebellum there was merely a membranous band passing transversely over the medulla oblongata, and connected on each side with a swelling of the size of a hazel-nut. The pons Varolii was entirely absent, the olivary bodies indistinct.‡

VI. *Of the cerebral hemispheres.*

The fact of the gradual developement of the cerebral hemispheres from the lower vertebrata up to man, and the coincidence of atrophy and absence of the convolutions on their surface with idiotcy, are alone sufficient to indicate that the seat of the higher intellectual faculties must be sought in this part of the encephalon. It has, however, been proved by direct experiment that such is their seat. The experiments of Flourens are here also especially instructive, and Hertwig has in the essential points done no more than confirm them. The hemispheres are insensible both to puncture and incisions. That part of the brain in which the sensations are converted into ideas, and the ideas hoarded up,

* See Weber, in the Nova Act. Nat. Cur. xiv. p. 111.

† Anat. Pathol. livr. xv. 18.

‡ See the representation of the parts in Cruveilhier, livr. xv.

to appear again, as it were, as shadows of the sensations, is itself devoid of sensibility. This result, confirmed by Hertwig, accords likewise with the phenomena observed in wounds of the head in man; for it has been very frequently remarked, when it has been necessary to separate protruded portions of the brain from the healthy part, that this has given rise to no sensation even in persons whose mind was perfectly clear. Wounds of the hemispheres give rise moreover to no convulsions; the only constant effect of a deep incision is blindness of the eye of the opposite side and a state of stupidity. Haller and Zinn had noticed that injury to the upper part of the cerebral hemispheres produces no muscular contractions. No contractions of muscles are excited, according to Flourens, by irritating the corpora striata or the optic thalami; and the same fact had been already ascertained by M. Lorrey with reference to the corpus callosum.

The general results of the experiments of Flourens and Hertwig on different animals, relative to the function of the cerebral hemispheres are very similar. I will recount the very interesting details of an experiment instituted by Flourens on a pigeon. The right hemisphere, being removed, the pigeon was found to be blind on the opposite side. The contractility of the iris, however, still continued (see page 831). There was a marked feebleness of all parts of the left half of the body. This, however, is, according to M. Flourens, a very variable phenomenon both as to its degree and duration. In all animals the powers soon recover their equilibrium, and the disproportion between the two sides disappears. The pigeon saw very well with the eye of the injured side; it heard, stood, walked, flew, and did not appear uneasy.

In another pigeon both cerebral hemispheres were removed; loss of vision immediately ensued, with general loss of power, which, however, was neither considerable nor persistent. The pigeon flew when it was thrown into the air; walked when it was pushed. The iris had its power of motion in both eyes; the animal was deaf, and it did not move spontaneously, but had constantly the manner of a sleeping animal, and when irritated it resembled in its motions an animal just awaking. In whatever position it was placed, it resumed its equilibrium; if laid upon the back, it got upon its feet again; water being put into its beak, it swallowed it; it resisted attempts to open its beak. M. Flourens likens the pigeon in this condition to an animal condemned to perpetual sleep, but deprived even of the faculty of dreaming. Experiments on mammalia were attended with similar results.

The experiments of Hertwig confirm M. Flourens' observations. Wounds of the hemispheres (in a dog) excited no pain, unless they extended to the base of the brain, when signs of pain were exhibited. M. Hertwig removed both hemispheres in a dog: the animal did not move from the spot voluntarily, but was thrown into a state of complete stupor;

if irritated, it moved a few steps, and then fell again to the ground in a sleepy state. It did not hear even the report of a pistol. M. Hertwig removed the upper part of the hemispheres in a pigeon; sight and hearing were abolished, and the animal sat in one spot as if asleep. He fed it: peas, if placed merely within the beak, were not swallowed; but they were, if laid upon the tongue, owing to reflex action; the muscles were but slightly enfeebled; the bird stood firmly, and flew when thrown into the air. This state endured for a fortnight, when the hearing and sensibility in a great measure returned; this pigeon lived three months. A hen, in which Hertwig had cut away both hemispheres nearly to the base of the brain, was found to be deprived of sight, hearing, taste, and smell; it sat constantly in one spot, and was as if dead until strongly roused, when it moved a few steps. The animal lived in this state of stupor, without its senses being restored, for three months.

M. Schoeps* has instituted similar experiments.

It is evident from these experiments, and from the effects of pressure on the cerebral hemispheres in man, that they are the seat of the mental functions; that in them the sensorial impressions are not merely perceived, but are converted into ideas; and that in them resides the power of directing the mind to particular sensorial impressions,—the faculty of attention. In what respect the medullary and the grey substance of the hemispheres differ with regard to function, we are quite ignorant. The capacity of the mind in different animals manifestly increases *pari passu* with the extension of the surface of the cerebral convolutions; but we have not the slightest knowledge of the nature of the influence exerted by the grey cortical substance into which the innumerable fibres which pass through the optic thalami at last radiate. We are ignorant of the nature of the change produced in the medullary fibres, in the cortical substance, or in the principle which animates it, when an idea makes an impression on the highly susceptible substance of this wonderful structure. We know only, that every idea is a permanent immutable impression in the brain, which may at any moment present itself anew if the mind be directed to it, if the "attention" be turned to it; and that it is merely the impossibility of the attention being occupied by many objects simultaneously, that causes each to be forgotten. All these latent ideas must be regarded as impressions on the brain which cannot be effaced. Lesions of the brain may annul a part or all these ideas. Thus, in such cases, persons have lost their memory for nouns, verbs, or even for the occurrences of certain periods of their life; and the memory thus lost has sometimes returned again. The direction of the mind to one single idea modifies the co-existence and disturbs the equilibrium of all the rest; hence, if the existent strength of the different latent ideas were known, it would be almost

* Meckel's Archiv. 1827.

possible to calculate what allied idea would be excited by another known image.

It is probable that there is in the brain a certain part or element set apart for the affections, the excitement of which causes every idea to acquire the intensity of emotion, and which, when very active, gives the simplest thought, even in dreams, the character of passion; but the existence of such a part or element cannot be strictly proved, nor its locality demonstrated. Still less can it be shown that, independent of such an element of the mind, the particular tendencies of the thoughts and passions have their special seat in distinct districts of the hemispheres. This view, advocated by Gall, which forms the ground-work of the doctrine of cranioscopy or phrenology, does not, it is true, involve any impossibility; but there are no facts calculated in the slightest measure to prove the correctness of the hypothesis generally, or the correctness of the details of the doctrine founded upon it. No part of the brain can be distinctly pointed out as the seat of memory, of imagination, &c. Memory may be lost as a consequence of lesion of the hemispheres at any part of their periphery; and the same is the case with regard to all the principal faculties or tendencies of the mind. On the other hand, with regard to the "faculties" set down by Gall, a part of which are totally unpsychological, we may at once exclude from the forum of scientific researches these arbitrary dogmas, which can never be proved. The remark made by Napoleon to Las Cases with reference to Gall's system of phrenology is very interesting: "He ascribes," said Napoleon, "to certain prominences, propensities and crimes which do not exist in nature, but are the growth of society, and are merely conventional. What would the organ of theft effect, if there were no property; the organ of drunkenness, if there were no spirituous liquors; or the organ of ambition, if there were no society?" Gall's system includes no organ of drunkenness; but still the remark is correct as far as regards the bad psychological foundation of the organs marked out by Gall. It does not, however, overturn the principle of phrenology; but only the mode in which it is carried out.

With regard to the principle, its possibility cannot, *à priori*, be denied; but experience shows that the system of organs proposed by Gall has no foundation, and the histories of injuries to the head are directly opposed to the existence of special regions of the brain destined for particular mental faculties. Not only may both the higher and lower intellectual faculties—as, reflection, imagination, fancy, and memory—be affected by lesion of any point on the surface of the hemispheres; but it has been frequently observed that different parts of the hemispheres can aid the action of other parts in the intellectual functions, and frequently where the removal of portions of the surface of the hemispheres has become necessary in the human subject, no change in their

moral and intellectual powers has ensued. M. Magendie is very right in placing cranioscopy in the same category with astrology and alchemy.

It appears, with regard to their action in the intellectual functions, that the one hemisphere can perform the office of the other. Cases have been observed, at least, in which permanent disease of one hemisphere has left the mind unimpaired; and Cruveilhier* has related a case of atrophy of the entire left half of the cerebrum in a man forty-two years of age, in which the atrophied hemisphere was only about half as large as the sound one, all its parts—the crus cerebri, corpus mammillare, thalamus opticus, corpus striatum, and lateral ventricle,—being all equally diminished in size, and nevertheless the mind was perfect. The size of the two halves of the cerebellum was nearly equal, the right being a little smaller than the left. In this case, the right side of the body had been from youth upwards partially paralysed, the man being still able to walk with a stick; the limbs of the weak side were wasted.

The commissures appear to be the cause of this unity of action of the two hemispheres. The influence of the corpus callosum is not quite certain; yet the presence of the corpus callosum and fornix would appear, from a case observed by Reil,† not to be necessary for the exercise of the lower mental faculties. In a woman whose intellects were dull, but who was nevertheless capable of common occupations, as of going on errands, the parts mentioned were wanting, but the other commissures were present. The coincidence of idiotcy with destruction of the corpus callosum in chronic hydrocephalus does not prove any connection between them, the disease being so complicated. But tumours and hydatids have been found attached to the corpus callosum in idiots; and La Peyronnie observed loss of memory attending lesion of that part of the brain.‡ Few direct experiments have been instituted with a view to determine the function of the corpus callosum. Saucerotte divided this part in a dog; stupor, with violent shaking and hiccough, were the result. The animal saw and heard, but had lost the sense of smell, and the sensibility of the ears, nose, and muscles.§ Rolando|| performed the same experiment on a goat. The animal stood for some time without moving, then became restless and ran forwards. It was kept two days; by degrees it became feeble, could scarcely rise on its legs, and its whole body trembled and was cold.

The functions of the pituitary and the pineal gland are, we may say, entirely unknown. Greding, it is true, frequently found disease of the pituitary gland in cases of mental affections; but, in such cases, disorganisations have been met with in all parts of the brain. Wenzel observed

* Livraison viii.

† Archiv. xi. 341.

‡ Cases of disease of the corpus callosum will be found collected in the works of Treviranus, Biologie, vi. p. 258; and Burdach, Op. cit.

§ See Burdach, Op. cit. iii. 486.

|| Saggio, &c. ii. 218.

disease of the pituitary gland frequently in epileptic subjects. The hypothesis of Descartes, that the pineal gland is the seat of the soul, has been long relinquished and forgotten. It is, according to Georget's observation, seldom affected in lunatics.*

The results of pathological anatomy can, however, never have more than a limited application to the physiology of the brain. We are unacquainted with the laws according to which the different parts of the organ participate in the affections of each other; and we can only in a general way regard as certain, that organic diseases in one part of the brain may induce changes in the function of other parts; but from these facts, and the results of pathological anatomy, we cannot always draw certain conclusions. Degenerations in the most various parts of the brain, which appear from experiment to have no immediate connection with the central organs of the sense of vision, nevertheless frequently cause blindness; and at this we must be the less surprised, since, even in diseases of the spinal cord, as tabes dorsalis, imperfect amaurosis is a frequent symptom.

The same remark applies to the relation of lesion of the different parts of the brain to mental diseases; the brains of insane persons frequently presenting degeneration in parts which are not the essential seat of the intellectual functions. Abundant confirmation of what we have here said is afforded by the collection of cases, and the calculations which Burdach has given, relative to the coincidence of disease of different parts of the brain with certain changes of the functions. It must be further remarked, that a chronic disease which acts merely by exerting pressure, and does not produce complete atrophy, may, by its gradual developement, prepare and accustom the compressed parts to its presence. Hence the great difference between the effects of chronic and those of sudden lesions of the brain. Thus important parts, such as the pons Varolii and crura cerebri, may be pressed upon, as in a case detailed by Cruveilhier,† by a pearl-like fatty tumour developing itself slowly, without their functions being essentially disturbed; in Cruveilhier's case, neither the power of motion nor sensation were affected.

VII. *Of the laws of action of the brain and spinal cord.*

We have here to consider the laws according to which nervous actions are propagated in the fibrous structure of the brain and spinal cord. Our knowledge is here as imperfect as it is complete with reference to the propagation of nervous action in the nerves. The primitive fibres of a nerve lying in the same sheath do not communicate their particular states from one to another; their action is propagated in each in an isolated manner from the periphery to the central organs, and from these back again to the periphery. If, as we have shown to be probable, these

* See Burdach, Op. cit. iii. p. 467.

† Anat. Pathol. livr. ii.

fibres be tubes containing nervous matter, the walls of the tubes would appear to have an insulating relation to the action of their contents. On the other hand, in the brain and spinal cord, the nervous matter is not contained in such distinct tubes; and between the fibres there is, particularly in the grey substance, a granular matter, which appears to facilitate the communication of influences from one fibre to another, even when no anastomosis of fibres exists. Hence, perhaps, the proneness to the propagation of a particular state of one part of the brain and spinal cord to another, and the phenomena of the reflection of impressions from the origin of sensitive roots to the contiguous motor roots of the nerves. Still, however, the propagation of nervous action in the fibres of the spinal cord generally follows more readily the direction of the fibres than any other course; otherwise the excitation of the roots of particular nerves to motor action, and the influence of the brain on the nerves of the opposite side of the spinal cord, would not be possible. The laws of action of the grey substance in the interior of the brain and spinal cord, and on the surface of the brain, are unknown. We must also be content to exclude from consideration the influence of the fibrous structure of the brain in all the intellectual functions.

Having already (at page 704) considered the phenomena of the reflection of nervous action from sensitive upon motor fibres through the medium of the spinal cord, no explanation of which is afforded by the structure of the latter organ or of the brain, we have here to investigate the motor apparatus of the central organs, and still more the paths of the propagation of sensations and motions—the crossing of the sensitive and motor influences, in them.

With regard to the motor apparatus, we must distinguish between those which, when wounded, excite convulsions, and those, mutilation of which diminishes the motor power without causing muscular spasms to ensue. This is an important distinction, which we owe to Flourens, and must, at a future period, have a great influence on the pathology of cerebral diseases. Experiments of M. Flourens and M. Hertwig show that the first class of motor apparatus includes only the corpora quadrigemina, the medulla oblongata, and the spinal cord; to the latter class belong all the other motor apparatus of the encephalon, namely, the optic thalami, the corpora striata, and the cerebrum generally as far as it has any motor influence, the pons Varolii and the cerebellum. By injuries inflicted on these parts, the power of motion is enfeebled, but no convulsions are excited; while injury to the medulla oblongata and spinal cord infallibly excites convulsions. Although, therefore, owing to the reaction of different parts of the brain on each other, it is probable that other parts than the corpora quadrigemina and medulla oblongata may, in disease, excite convulsions by sympathy; and, indeed, pathology teaches us that such is the case; yet, from the facts above mentioned,

we may infer that, when the power of motion of the limbs is defective from disease in the central organs, the cause may be seated either in the corpus striatum, thalamus opticus, hemispheres, pons, cerebellum, medulla oblongata, or medulla spinalis; but that in cases of convulsions, or convulsion with paralysis dependent on disease of the brain or spinal cord, the seat of the disease is more likely to be the corpora quadrigemina, spinal cord, or medulla oblongata, than the other parts of the nervous centres.

Another important circumstance with reference to the laws of action of the brain and spinal cord, is the crossing of the nervous actions in them. From experiments on animals, and pathological observations, it results that lesions of the spinal cord and medulla oblongata always cause convulsions or paralysis on the same side of the body. This is quite intelligible in the case of the spinal cord, for in it there is no decussation of the fibres of the two lateral halves; but, with reference to the medulla oblongata, the above result of the experiments of Flourens and Hertwig is not perfectly consonant with the anatomical structure of the part; for since, in the medulla oblongata, the fibres of the corpora pyramidalia at least decussate, while those of the other fasciculi continue their course on the same side of the spinal cord, it would be expected that, according to the part of the medulla oblongata affected by the lesion, the consequences would be observed on the opposite or on the same side of the body. M. Lorrey had, indeed, observed that when wounds were inflicted upon the medulla oblongata, the convulsions were constantly on the same, the paralysis on the opposite side of the body. To this result, however, those of the experiments of Flourens and Hertwig are directly opposed; but we must recollect that their experiments were instituted principally on the lateral columns only which do not decussate; and it is very probable that, if the corpora pyramidalia be wounded above the decussation of the fibres, the effects produced would be seen on the opposite side of the body.

Injuries inflicted on the cerebellum, the corpora quadrigemina, and cerebrum, are always productive of loss of power on the opposite side; mutilation of the hemispheres or optic lobes, of blindness of the eye of the opposite side: this is the general result of the experiments of Flourens and Hertwig. With reference to the cerebral hemispheres, it had been already proved, partly by experiment, and partly by pathological observations, by Caldani, Arnemann, Valsalva, Wenzel, and others.* M. Magendie makes the same remark with regard to the cerebral hemispheres; and by extirpation of one eye in birds he has produced atrophy of the opposite optic lobe. The influence of injury of the corpora quadrigemina is, according to M. Flourens, produced both in the anterior and the posterior direction on the opposite side; anteriorly

* See Treviranus, Biologie, vi. p. 117.—Burdach, loc. cit. iii. p. 365.

on the eyes, posteriorly on the other parts of the body. Pathological observations confirm, for the most part, this result; the rare exceptions which have been met with are collected by Treviranus and Burdach. According to Burdach's calculation, in two hundred and sixty-eight cases of lesion of one side of the brain, ten presented paralysis on both sides of the body, two hundred and fifty-eight hemiplegia; and in only fifteen of these was the paralysis on the same side as the lesion. The convulsions were in twenty-five cases on the same side as the disease; in three cases, on the opposite side.

These facts afford an explanation of the origin of the dogma which has prevailed since the time of Hippocrates, namely, that in wounds of the brain the convulsions occur on the wounded, the paralysis on the opposite side. In fact, if the wound have a certain direction, it may produce both these effects at the same time, by implicating different parts. No one has contributed to elucidate these difficulties so much as M. Flourens: he has shown that injury of the spinal cord and medulla oblongata causes paralysis and convulsions on the same side, and injury of the corpora quadrigemina paralysis and convulsions on the opposite side; while injury of the thalami, corpora striata, and hemispheres of the cerebrum and cerebellum, induces paralysis on the opposite side of the body without convulsions. If, now, both cerebellum and medulla oblongata were wounded simultaneously on the same side, paralytic weakness of the opposite side, and convulsions and paralysis of the same side as the injury, were the consequence. Although Flourens* has, by his experiments, thrown much light on the cross effects of lesions which give rise to paralysis and convulsions, yet he appears to have gone too far in concluding that lesions on one side of the cerebrum cannot give rise to convulsions on the same side of the body; for it is very remarkable that in the cases of lesion of one side of the brain, collected by Burdach, convulsions occurred in twenty-five cases on the same side of the body as the disease; in three cases only on the opposite side: of these cases those are, with reference to our inquiry, especially important in which there wa: paralysis on the opposite side, with the convulsions on the same side as the cerebral lesion. In cases of lesion of one corpus striatum, there were, with thirty-six instances of paralysis of the opposite side of the body, convulsions of the same side as the disease in six instances, and in no instances convulsions of the opposite side. This appears to be very much in favour of the old opinion that, when convulsions occur in cases of lesion of one side of the brain, with paralysis of the opposite side of the body, they are most prone to affect the same side as that on which the cerebral lesion is seated.

When the decussation of the corpora pyramidalia of the medulla oblongata became known, the explanation of the cross actions of the

* Sur le Syst. Nerveux, p. 110.

brain by this structure was too obvious not to be immediately adopted; and the concurrence of the cross influence of the brain with this structure of the corpora pyramidalia proves that these are the parts in the medulla oblongata which are principally engaged in conducting the motor influence from the brain to the trunk.

There is greater difficulty in explaining the modes of action of the brain in its influence on the cerebral nerves of the opposite or same side of the body. For since these nerves arise, for the most part, above the point of decussation of the pyramidal bodies, the cause of the cross action of injuries of the brain on these nerves must have some other seat; and, what involves the question in still more difficulty is, that in man the nerve of the same side is as frequently affected as that of the opposite side in cases of cerebral lesion. For a detail of facts, I must refer to Burdach's work, in which an admirable industry is displayed. In twenty-eight cases of cerebral lesion of one side, the muscles of the opposite side of the face were paralysed; in ten cases, those of the same side. Paralysis of the eyelid was in six cases on the same side; in five, on the opposite. Paralysis of the muscles of the eye-ball, in eight cases on the same side; in four, on the opposite. Paralysis of the iris, in five cases on the same side; in five also, on the opposite.* The tongue is generally drawn towards the paralysed side of the face.

Cerebral lesions in man as frequently cause paralysis of the retina of the same as of that of the opposite side. Since each optic nerve derives a root from both hemispheres, this is in some measure intelligible. But, according to the theory of the optic nerves, a lesion of one side of the brain ought not to produce entire blindness of either retina, but merely paralysis of one half of each, (see page 705,) so as to cause blindness of the right or left side of the two eyes, which has indeed been observed as a temporary symptom.† This, however, is not the ordinary effect of paralysis of one side of the brain; usually, either one eye or the other is entirely blinded. It is remarkable that in animals lesion of one side of the brain always causes blindness of the opposite eye; the difference of this result, from what takes place in the human subject, is explained by the structure of the commissure of the optic nerves in animals: nearly all the fibres of the two nerves decussate. This structure is necessary in them; since, from the direction of their eyes, the greater part of the field of vision of each embraces entirely different objects. Only the objects in the middle line throw their image on both retinæ; a small part only, therefore, of the retina of the one eye is identical in sensation with that of the other, and receives its fibres from the same side of the brain. (See page 703.)

From the preceding facts, relative to the laws of action of the brain, and from those already given relative to the action of the spinal cord,

* Burdach, op. cit. iii. p. 372. † See Müller's Physiol. des Gesichtsinnes, p. 93.

we may form a classification of the different kinds of paralysis and convulsions, with reference to the seat of the cause which produces them.

1. *Paralyses.*—Paralysis may have its seat in individual nerves, and not in the brain and spinal cord; or it may be the result of disease in the latter parts. The local paralytic affections of nerves arise from any cause which destroys their power of propagating nervous action; as, rheumatic affections, division, tumours, &c. The greater number of paralytic affections, however, have their cause seated in the central organs, the brain and spinal cord. In these cases, the paralysis affects either a vertical half of the body, hemiplegia, or a horizontal half, paraplegia. In the first form, the cause has its seat on one side of the brain and spinal cord: in the second form, it is generally seated on both sides, but may be on one side only; for paraplegia is often produced when the disease implicates one side only of the brain.

a. Paralysis from disease of the spinal cord.—In this class of cases, the seat of the disease is generally indicated by the extent of the parts paralysed. If merely the lower extremities and sphincters have lost their power, it is generally only the lowest portion of the cord that is affected; if the disease be seated at a higher point, a larger part of the body will be paralysed. If the disease affect the cord below the origin of the fourth cervical nerve, the paralysis will embrace the upper extremities, alone or together with all the parts below them, but not the phrenic nerve. If lesion affect the cord at a higher point than this, the phrenic nerve also is deprived of its power. Lesion of the medulla oblongata paralyses the cerebral nerves which arise from it, as well as the whole trunk. I am acquainted with a case of disease of the medulla oblongata from the pressure of a small tumour, in which imperfect paralysis gradually affected all the muscles of the body simultaneously; the upper and lower extremities, the tongue, eye, and face, were all partially paralysed. In the majority of cases of paralysis from disease of the spinal cord, the seat of the lesion is indicated by the extent to which the paralysis extends upwards. Injury to the lumbar portion of the cord constantly paralyses the lower, and never the upper extremities. If the arms be paralysed, the lesion must have its seat above the origin of the brachial nerves; but the lower limbs are in this case not necessarily affected. The effects of disease of the spinal cord are always seated on the same side as the lesion. If it be the sensibility of the limbs that is lost, the cause most probably, but not certainly, has its seat in the posterior columns of the cord; if it be motion which is lost, the anterior columns are more frequently, but not constantly, the seat of the lesion. (See page 800.) Paralysis from disease of the spinal cord is sometimes complete, sometimes incomplete: when complete, the propagation of cerebral influence is wholly interrupted at some point; when incomplete, the influence of the will is still transmitted to the

muscles, but the intensity of the motor power is lost; this is what is observed in atrophy of the spinal cord, or tabes dorsalis.

b. Paralysis from disease of the encephalon.—The paralytic affections of this class may present themselves in any part of the trunk, in the face as well as in the upper and lower extremities. Paralysis of the muscles of the leg, as of the sphincters, may, therefore, be the result of disease either of the brain or spinal cord. It may be inferred to depend on disease in the brain, when other parts or functions are affected, which are under the influence of cerebral nerves; as, for example, the muscles of the eye, the functions of vision, and hearing, speech, or the movements of the tongue, the muscles of the face, &c. The paralysis may consist likewise either of loss of motion or of loss of sensibility, or of both. Paralysis of the motor power may depend on lesion of the corpora striata, the optic thalami, the investments of the cerebral hemispheres themselves, the corpora quadrigemina, the pons, the medulla oblongata, or the cerebellum. Serres, Bouillaud, and Pinel-Grand-Champ maintain that they have found paralysis of the upper extremities more frequently dependent on disease of the thalami optici; paralysis of the lower extremities, on disease of the corpora striata: this is by no means an established fact. When it is the sensibility of the parts that is paralysed, the seat of the disease may be very various. Blindness is most frequently caused by degeneration of the cerebral hemispheres, particularly of the optic thalami, or by disease of the corpora quadrigemina. Loss of common sensation is most frequent in disease of the medulla oblongata. Paralysis from disease within the head may likewise be complete or incomplete; the loss of motor power is most prone to be complete when the lesion is seated in the corpora striata, optic thalami, crura cerebri, or pons. Incomplete paralysis is most generally dependent on disease of the cerebral hemispheres, or of the cerebellum. The paralysis is most apt to be attended with convulsions or spasmodic contractions of muscles when the corpora quadrigemina, the medulla oblongata, or the parts at the base of the cerebrum, are the seat of the disease. Paralysis of the trunk is generally on the opposite side to the disease; paralytic affections of the head as frequently on the same as on the opposite side.

2. *Convulsions.*—The cause of convulsions may be seated in the nerves themselves, in the brain, or in the spinal cord.

a. From disease of the nerves.—Such are the convulsions caused by the reflection on motor nerves, by the spinal cord and brain, of an influence communicated to them, either from local diseases of nerves, as tumours, or neuralgic affections; from any strong impression on sensitive nerves; or, in children, from any local disease.

b. From disease of the spinal cord.—These are regulated by the same laws as paralytic affections from disease of the same part.

c. From disease of the brain.—These also observe the same laws as paralysis from cerebral disease. It is, however, to be remarked, that lesions of the cerebral hemispheres, the cerebellum, and the pons Varolii, are more prone to cause paralysis; lesions of the corpora quadrigemina and medulla oblongata, to cause both paralysis and convulsions.

Having thus investigated the laws of the propagation of nervous influences in the brain and spinal cord, we have, in the last place, to consider some phenomena resulting from disturbance of the equilibrium in the actions of the brain. Division of certain parts of the encephalon gives rise to phenomena which seem to indicate a disturbance in the equilibrium between forces opposed to each other in the two sides of the brain. The phenomena form a class of a quite peculiar character.

A certain part of the brain being divided, the action of the corresponding part of the other side becomes exaggerated. A vertical section of the pons Varolii on one side causes the animal to make a number of revolutions towards the same side; and this motion is arrested by dividing the pons on the other side. M. Hertwig confirms the result of M. Magendie's experiments, as to the rolling motion of the animal excited by division of the pons on one side; and states, moreover, that the eyes were turned from their ordinary position, one upwards, the other downwards. A transverse section of the pons being made, the dog could stand, but could not advance a step without falling; voluntary movements could still be performed, and sensation was perfect.

Division of the crura cerebelli (processus ad pontem) was likewise found by M. Magendie to cause the animal to roll upon its axis towards the side on which the wound was inflicted; sometimes as many as sixty revolutions were made in a minute; and he states that he has seen them continue for a week without intermission.

After the removal of both corpora striata, the animals manifested an irresistible impulse to dart forwards, even when vision was lost.

Magendie has likewise observed that injuries of the cerebellum in mammalia and birds cause a tendency to retrograde movement to be exerted. He observed the same phenomenon after wounds had been inflicted on the medulla oblongata; pigeons, in which he had thrust a needle into that part of the encephalon, were observed by him for more than a month to walk backwards, never forwards; he states that they actually flew backwards.

M. Magendie has observed, lastly, that certain kinds of injury to the medulla oblongata are followed by the animals moving in a circle, as on a riding course. He performed the experiment in a rabbit three or four months old; he exposed the fourth ventricle, raised the cerebellum, and then made a perpendicular section into the floor of the ventricle at the distance of $1\frac{1}{4}$ to $1\frac{4}{5}$ of a line from the mesial line: when the section

was made on the right side, the animal turned towards the right; when on the left, it turned towards the left.

From the above important facts M. Magendie infers the existence in the brain of certain impulses by which the animal is necessitated to move in certain directions; by one forwards, by another backwards, by a third to the right, and by a fourth to the left: the detail of these motions he supposed to be directed by volition; and he imagines that in the normal state of the body the different impulses balance each other. Whether this explanation of the phenomena be the correct one, cannot in the present state of our knowledge be determined. It may easily be conceived that an animal might be impelled to such movements, if from the nature of the injury to the brain a certain motion of the nervous principle in one direction should take place in it, giving him the sensation of giddiness,—that is to say, of surrounding objects, or of his own body, moving round,—when he would endeavour to resist this apparent movement, or would follow it.

The phenomena last considered relate to the motor functions, but there are similar phenomena of the sensorial kind. Certain influences acting on the brain give rise, not to rotatory motions, but to sensations of rotation. These are the revolving sensations of vertigo, of which we are principally conscious by the sense of vision. It is a well-known fact that if any person turns round quickly upon his own axis for a short time, he not only begins to lose his recollection, but also, when he ceases to move, seems to see the objects around him still revolving in the same direction. Purkinje has made some very curious observations relative to this phenomenon. It would appear from his experiments that the direction which the revolution of the images shall take can be regulated by the position of the body, and particularly of the head while turning round, and by the position of it afterwards when we have ceased to move round. It is only when the experimentor has kept his head in the ordinary vertical position while turning round, that afterwards, when he stands still with his head upright, the objects appear to revolve in the horizontal direction. If while turning he hold his head with the occiput upwards, and then raise it when he stands still, the apparent motion is like that of a wheel placed vertically revolving around its axis. And thus, according to the difference in the position of the head when turning and when standing still afterwards, the direction of the apparent revolving motion can be altered. If, however, the body lying upon a disk is made to revolve with this disk, an apparent motion of objects in tangents is perceived. It results from a repetition of these experiments that the plane of the head, regarded as a sphere, around the axis of which the real motion was performed, determines the plane in which the apparent motions afterwards seem to take place when the motion of the body has ceased, and the head has assumed another position. From

this remarkable result Purkinje infers that turning of the head and whole body gives to the particles of the brain the same tendencies to particular motions as the particles of a revolving disk receive, and that this disturbance of their state of rest is manifested by the apparent movements of vertigo. We might perhaps better explain the phenomenon by supposing it to result from the impressions of the blood in a particular direction on the cerebral substance. It is possible, however, that the revolving motion of the body may cause an aberration of a more subtile principle than the particles of the cerebral substance or blood,—in fact, an aberration of the nervous principle itself, such as affects the sensorium so as to produce the apparent motions of objects. It is certain that narcotic substances give rise to the vertiginous sensations of the motions of objects, although they produce no mechanical disturbance of the brain. However they be explained, these sensorial phenomena afford a very interesting parallel to the revolving motions of the body, caused by a disturbance of the equilibrium of nervous actions in motor parts of the brain.